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George Taylor Porritt's 19th and early 20th century observations on industrial melanism in moths in South West Yorkshire, and their continuing relevance to a long-running debate – *Geoffrey Fryer*

Lichen Flora of the West Yorkshire Conurbation: a conspectus – *M.R.D. Seaward*

A Naturalist in Wartime: John Buxton's Pioneering Study of the Redstart – *Kristin Johnson*

The Northern Bottlenose Whale *Hyperoodon ampullatus* (Odontoceti: Ziphiidae) in Yorkshire Waters, with notes on its migration, feeding ecology and the discovery of photographs of the Stranding at Spurn 28 July 1930 – *Colin A. Howes and Peter Crowther*

Sperm Whale *Physeter macrocephalus* Strandings on the Cleveland, North Yorkshire and Humber Coastlines – *Colin A. Howes*

Robert Francis Dickens 1918-2010

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A manuscript plus disc (WORD format) OR two manuscripts, typed double-spaced on one side of the paper only with margins at top and left-hand at least 2.5cm wide, should be submitted. Latin names of genera and species, but nothing else, should be in italics. S.I. Units should be used wherever possible. Authors must ensure that their references are accurately cited, and that the titles of the journals are correctly abbreviated. Volumes of *The Naturalist* for the years 1886 to 1975 have been retrospectively numbered 11 to 100 to accord with numbering before and after this period (see YNU *Bulletin* no. 3, pp. 21-22 1985); please cite these volume numbers in all references. Table and text-figures should be prepared on separate sheets of paper. Drawings and graphs, drawn about twice the linear size they are to appear, should be in jet-black Indian ink, and legends should not be written on the figures. Photographic illustrations, normally black and white, will be considered for inclusion. **Publishable manuscripts not conforming to the above requirements will be returned for alteration.**

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EDITORIAL

The Naturalist, one of Britain's longest-running natural history journals, was first issued in August 1875, and the Yorkshire Naturalists' Union is justifiably proud of it. Until April 1942, *The Naturalist* appeared monthly with no interruptions, but since then it has been issued quarterly. By December 2010, 1075 issues (in 135 volumes) of *The Naturalist* have been published, during which time it has had only ten editors:

	Dates	Issues	
C.P.Hobkirk & G.T.Porritt	1875-1884	1-108	(108)
W.Denison Roebuck & W.Eagle-Clarke	1884-1888	109-161	(53)
W.Denison Roebuck	1889-1902	162-329	(168)
T.Sheppard & T.W.Woodhead	1903-1932	330-689	(360)
W.H.Pearsall & W.R.Grist	1933-1942	690-803	(114)
W.R.Grist & W.A.Sledge	1943-1947	804-823	(20)
W.A.Sledge	1948-1974	824-931	(108)
W.A.Sledge & M.R.D.Seaward	1975	932-935	(4)
M.R.D.Seaward	1976-2010	936-1075	(140)

The current issue marks the end of an era, not only for the journal, which will assume a new format and combine the "old" *Naturalist* with the *Bulletin*, but also for its editor who will be stepping down after 36 years. During this time it has been a privilege and a pleasure to serve the YNU in this capacity and to maintain the reputation of its journal, which was described ten years ago by the author of *The Aurelian Legacy* as having "...achieved an influence far transcending local boundaries".

Naturally, I would have wished to maintain my editorship, but the YNU moves on and its Executive Committee has thought it expedient to cater for those little interested in a more academic journal in which all articles are peer reviewed.

I extend my deep gratitude to all those who have contributed to *The Naturalist* over the past four decades, and also to the readership which has been considerably extended, not only nationally but worldwide, through library, college and university subscriptions, in addition to microfilm production and abstracting services. Work on a quarterly journal never ceases, and at times I have been unable to undertake other commissions and interests outside of those connected with my profession. Nevertheless, it gives me pride to record that the few criticisms received over the many years as Editor have been far outweighed by the number of appreciative reports I have received from contributors and readers who have made my task a most enjoyable experience.

Mark Seaward
University of Bradford

December 2010

BOOK REVIEWS

Birds of Cleveland by **Martin A. Blick**. Pp. 352, incl. numerous line drawings & photographs. Tees Valley Wildlife Trust. 2010. £20.00 softback.

This book is the result of the author's dedicated association with the region for over 40 years. The Teesmouth Bird Club, founded in 1960, has collected a vast number of records, published in its annual reports, from which the author has gleaned much of the material detailed in the systematic list. Cleveland has a variety of habitats, ranging from high, rugged sea cliffs, moorland and conifer forests to the flat marshes bordering the Tees, an area which has become heavily industrialised. Nevertheless, this area has, over the years, produced a wealth of interesting birds.

Since the early part of the 20th century when T.H. Nelson, from his home in Redcar, roamed the Teesmouth, gun in hand, to study its birdlife, the lonely windswept beaches, dunes and marshes have changed dramatically with increasing industrialisation; fortunately, several areas have persisted and birds have the ability to seek these out whilst on migration. The Royal Society for the Protection of Birds has taken over a large part of the wetland and created a landmark reserve at Saltholme Pools, thus ensuring the protection of what is a major part of this important region.

The author has encapsulated much of the region's history, together with chapters on topography, geology and the various habitats. There is a detailed monthly summary of likely bird occurrences and a most informative list of 84 birdwatching sites. The systematic list details all the 362 species recorded in the county of Cleveland up to the end of 2007, including those from the 19th century. A list of 54 species of presumed escaped birds makes fascinating reading and the book concludes with a glossary of terms and a full list of references. The author is to be congratulated on what is a very well written and attractively produced avifauna which will stand as an authoritative reference work for many years to come. Anyone interested in the birds of this part of north-east England should buy it without delay.

JRM

Tracks and Signs of Insects and other Invertebrates. A Guide to North American Species by C. Eiseman, C. and N. Charney. Pp. 582. Stackpole Books. 2010. $39.95 [c. £25.00] paperback.

Although at first glance this book may appear to be intended for US naturalists, it also provides a plethora of information which equally applicable to our own invertebrate fauna. When asked to review this book I was at first inclined to view it as just another 'coffee table' publication for the non-specialist. I was very much mistaken. It is something else entirely and with almost a thousand colour plates throughout, coupled with good technical descriptions of the myriad of tracks and signs left by invertebrates, I was pleasantly surprised and thoroughly enjoyed reviewing this fine publication. The colour plates and technical descriptions are excellent, and are further accompanied by notes on the ecology of a wide range of species illustrating the enormous range and diversity of invertebrate field signs.

Although a little pricey, this publication deserves a place on the bookshelf of anyone interested in invertebrates, whether a novice or a specialist. Thoroughly recommended, being enjoyable and immensely informative.

DGH

GEORGE TAYLOR PORRITT'S 19TH AND EARLY 20TH CENTURY OBSERVATIONS ON INDUSTRIAL MELANISM IN MOTHS IN SOUTH WEST YORKSHIRE, AND THEIR CONTINUING RELEVANCE TO A LONG-RUNNING DEBATE

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INTRODUCTION

In 1906, George Taylor Porritt (1848-1927) presented to the British Association for the Advancement of Science, which that year met in York, an account of the origin and spread of what is now referred to as industrial melanism in more than 40 species of moths in South West Yorkshire, and especially in the Huddersfield area. Here rapid industrialisation in the 19th century, which involved the burning of vast quantities of coal, led to the production of much smoke and the deposition of soot which blackened both natural and man-made features of the environment. This, and the emission of toxins, perhaps especially sulphur dioxide, had deleterious effects on the local Lepidoptera. Some species suffered extinction (Fryer & Lucas, 2001). Several species of moths reacted to these conditions by synthesising an abundance of the dark pigment, melanin, which rendered them dark or almost black in colour. Of these events, Porritt and his fellow lepidopterists were from the very beginning, witnesses. His account of events, published in the following year (Porritt, 1907), is a truly remarkable, but sadly neglected, document on a subject that subsequently became the focus of an immense body of work. Its historical interest is alone sufficient to merit attention, but the continuing relevance to more recent work of his observations and how he interpreted them, are even more demanding of such. In drawing attention to these matters it is, however, not always possible to integrate his findings smoothly with later conceptions; not least because, although industrial melanism has now been the subject of numerous investigations, it has evoked divergent views, some of which are still controversial. Herein indeed his observations on the earliest phases of the phenomenon are of particular relevance and interest. They include indisputable facts, recorded at that time, that have a direct bearing on how events should be interpreted but which have hitherto not received the attention they deserve. Like observations that he recorded even earlier, some of them cast serious doubt on the validity of key assumptions that have been made in the interpretation of a much studied and widely publicised phenomenon that has long been regarded as an outstanding example of evolution in action.

WHAT PORRITT SAW AND RECORDED

The story begins in 1848, appropriately the year of Porritt's birth, by the finding in the vicinity of Manchester of a Peppered Moth, *Biston* (then *Amphydasis*) *betularia*, which, instead of having almost white wings whose dorsal surface was mottled with black, had fore wings that were so densely pigmented by melanin as to be almost black, and hind wings that were similarly, but less intensely, pigmented. Shortly thereafter further melanic individuals (known as the *carbonaria* form) were found and, in what in the context of evolution was an amazingly short period of time, largely replaced the normal form over a wide region in industrial parts of East Lancashire and South West Yorkshire. Indeed, by the end of the century, c. 98% of individuals in these areas were melanic. As is now known, only one gene is involved but there are five alleles at the locus concerned. One of these, C – *carbonaria* – is fully dominant to all the others and is the one that is overwhelmingly involved in industrial melanism in northern England.

While occasional melanic individuals of a few species of moths had long been known to occur sporadically in the Huddersfield area, as can be the case anywhere, Porritt noted how *B. betularia* was the first regularly to display melanism there. He made it perfectly clear that while the manifestation and increase in incidence of the phenomenon in this species had taken place "within the memory of the present generation of entomologists" –

of whom the Huddersfield area was home to several – "it remained for years practically our only representative of true melanism". This point calls for emphasis. He also graphically recorded the increase in incidence of melanic individuals. Even within his own collecting experience (which embraced the previous 40 years or so) it had been regarded as good fortune to find a melanic individual among those of the normal 'peppered' form. By 1906, however, the melanic form had almost entirely replaced the original form in the South West Riding, and of the latter he had seen only one example in the Huddersfield area in the last nine or ten years. Even more remarkable, from about 1880 onward, he and his fellow lepidopterists began to notice that several other species were producing dark forms in increasing numbers, "some of them rather rapidly". That is, not until some 30 years or so after the phenomenon had manifested itself in the Peppered Moth, was melanism – in his words the presence of "black or nearly black" individuals – noticed in other species. At that time, however, it seemed to develop in several species "almost simultaneously". Thanks to Porritt's account we know that the first four such were the Pale Brindled Beauty *Apocheima* (then *Phigalia*) *pilosaria,* the Engrailed, *Ectropis bistortata* (then *Tephrosia biundularia*), the Dotted Border, *Agriopus marginaria* (then *Hybernia progemmaria*), all members of the Geometridae, and a 'microlepidopteran', *Diurnea fagella*. Exactly when *D. fagella* became melanic was less certain than the rest (see below). The next species in which melanism was recorded was another geometrid, the Mottled Beauty, *Alcis* (then *Boarmia*) *repandata*, of which, however, in 1887, a large proportion of individuals were black, which suggests its initiation some time before this. Porritt also knew of two black individuals of this species that had been collected in the Huddersfield area in about 1850. Whether these were precursors of the wave of melanism that was to follow or isolated mutants will for ever remain unknown.

Another example of melanism, that made its appearance in the 1860s, which he studied in considerable detail, he regarded as completely different from the rest. This was a mutant of the geometrid Magpie Moth, *Abraxas grossulariata* whose wings were almost black, that was described by Varley (1865) and subsequently designated ab. *varleyata* by Porritt. This was always very rare, and he stressed that "there has been *no* increase" in its incidence. What he did consider to be the industrial melanic form of this species was the ab. *nigrosparsata* which made its appearance in the area in the early years of the 20th century.

Subsequently, in more and more species, hitherto pale and still so in many places elsewhere, melanic individuals began to appear with increasing regularity. For reasons that will become apparent, it is important to appreciate that, inevitably, members of this assemblage differed much in habits. Particularly relevant is that most of those involved are nocturnal, and their behaviour by day is very relevant to arguments that follow. However, the Common Heath, *Ematurga* (then *Fidonia*) *atomaria*, is diurnal, and so too are males of the Northern Eggar, *Lasiocampa* (then *Bombyx*) *quercus callunae*, while females of the Muslin Moth *Diaphora* (then *Arctia*) *mendica* also sometimes fly in the sunshine. Each species has particular behavioural attributes, and all differ in various ways from *B. betularia*, on the basis of whose behaviour, or alleged behaviour, many generalisations about the phenomenon of industrial melanism have been made. What is particularly important to appreciate is that Porritt recognised that not all species became melanic in an identical manner. After about 1880, in more than 20 species of moths of which only pale forms had previously been known in that area of Yorkshire, black or nearly black individuals began to appear. These he enumerated. He also recorded that in more than 20 other species, also listed, individuals that were darker than formerly were so frequently encountered as to indicate that "they too are being influenced towards the same end". That is, he provided information on the spread of melanism by two different mechanisms. In some cases replacement of the usual (or 'typical') by melanic forms took place in the manner now familiar in the Peppered Moth, where the nature of the individual (the phenotype) – whether melanic or typical – is determined by a single gene. However, in other cases the same end was achieved by the *gradual darkening* of members of the

population over several years, which clearly involved a different – and more complex – genetic mechanism. Moreover, and particularly noteworthy, his observations showed that in some species, different mechanisms were operating in the two sexes! He also emphasised the rapidity of these changes and suggested that dark forms of many of the species concerned promised, at no distant date, entirely to oust what he called the "old ordinary pale forms".

As perhaps the most striking example of rapid change of the first type – uncomplicated by differences between the sexes – Porritt cited a geometrid moth, the Mottled Grey, *Colostegia* (then *Larentia*) *multistrigaria* of which no dark individual had been seen in his area until as recently as about 1895. Since then, as Morley (1906) reported from Skelmanthorpe, less than seven miles SE of Huddersfield, in 10 years the melanic form had so increased in numbers there that he believed that the local population would soon be entirely black, and Porritt's own observations strongly supported this opinion. Moreover, he recounted a very similar history for another geometrid, the Scalloped Hazel, *Odontopera bidentata,* "always regarded as one of our most constant species" which was being replaced by a black form at a more or less similar rate in some areas.

Two other geometrids, the Pale Brindled Beauty, *Apocheima pilosaria*, whose females are apterous (wingless) and the Dotted Border, *Agriopus marginaria,* which has brachypterous females, were among the very earliest species in which a replacement of pale by melanic individuals was observed. These displayed a different pattern of events which show how complex some of the changes really were. Porritt dated the advent of their melanism to about 1880 and reported that almost all the females were black "for some time" *before* 1886, which indicates the operation of a single gene as in the Peppered Moth, though the rate of change was dramatically more rapid than in that species. If selection was indeed the explanation, it was not only more intense, but the selective advantage of melanic over normal females must have been enormous. The rate of change was even faster than in the Mottled Grey, and perhaps as much as ten times as fast as in the Peppered Moth! Very specifically he recorded that the females became black before the males "began to darken", and, as he continued, "certain it is that they were so when we first began to notice that the males were rapidly becoming darker. At first the unicolorous black males were not common, but there were plenty of intermediates, and year by year the dark ones increased, and now in the case of [the Dotted Border] in some districts largely predominate". In *A. pilosaria* a dominant melanic form (*monacharia*) and an intermediate are now recognised in the male whereas there are no intermediates in the female. As Porritt made absolutely clear more than a century ago, the mechanism is different in the two sexes. Although the rate of change was less rapid in the males than in the females – it was about 25 years before virtually all the males of *A. marginaria* were completely black, compared with about five or six years in females – this was nevertheless a rapid rate of change. These remarkable findings have not received the recognition they deserve.

Another example of rapid change, which illustrates that the phenomenon arose in moths of widely different genetic affinities, was provided by the microlepidopteran *Diurnea fagella* whose short-winged females are flightless. It also shows how easily even a dramatic event could escape notice. Although Porritt had not paid much attention to microlepidopterans he happened to have been very familiar with this species some 20 years earlier and knew that at that time all individuals of both sexes were essentially pale grey in colour. In 1886, he had need for representatives of this moth and in late April went into a wood after dark and quickly picked from the trunks of Oak trees, where "both sexes were in profusion", 120 individuals, of which "probably 50 were females". Of these, only two, one of each sex, were pale; the rest were melanic. There had been a dramatic increase in the incidence of melanism that had changed the nature of the phenotype of most individuals of the local population of *D. fagella* in less than 20 years.

To anticipate arguments relating to the *role* of melanism, Porrritt then emphasised that the flightless females of the two geometrid moths, and those of *D. fagella,* "do *not* much affect tree trunks in the daytime", and roughly quantified this statement by adding that

"probably not near 1% of the number that can be found there after dark with the aid of a lamp do so". Nor did more than a very few males of *A. marginaria* frequent tree trunks in the daytime, but males of *A. pilosaria* did so. He then went on to say that the by then usually, but not universally, accepted theory, propagated especially by Tutt, though he was not the originator of the idea, was that in the soot-blackened environment of industrial areas the normal pale forms of these moths are much more conspicuous when settled than are melanic individuals, and that the latter are thereby better protected against attack by predatory birds. With *Biston betularia* particularly in mind, resting in exposed situations by day was usually assumed by those who held this belief. However, while not denying that melanism may in some cases be protective, he went on to point out that he did not believe that birds fed to any extent on the larger moths, and that the Nightjar, that does, only takes them on the wing where similarity to a dark background, such as a tree trunk, would be of no consequence, and that the same applies to bats, which are now known to employ echo location for the detection of prey, as well as for navigation. In view of the controversy about whether birds are important predators of moths (or are of scant significance in this respect) Porritt's early rejection of this belief – an opinion that he never changed – deserves emphasis. He also pointed out that there seemed to be no evidence of any enemies that systematically search tree trunks for large species of moths, and that many of the species that had become melanic, such as the Mottled Grey, *Colostegia multistrigaria,* or the flightless females of the three species just mentioned, do not frequent tree trunks in the daytime. Indeed, from personal experience he was able to say that *C. multistrigaria* hides among grasses and other green herbage by day in places where the vegetation is so thick that any correspondence in colour with the underlying soil would be of little value as camouflage. It is, as he put it "absolutely out of evidence until dusk" but after dark can be found with the aid of a lamp sitting on walls. In such cases as this and the flightless females of the three species just mentioned, melanism clearly does nothing to protect them from predatory birds. Certainly these species, and others to be mentioned later, are almost entirely exempt from the attention of such predators. Worth noting too is that adults of *Apocheima pilosaria* are active from January (occasionally earlier) to March, when protection from birds is least needed as all summer-visiting insect eaters are absent and short days reduce searching time.

The impression of the habits of industrial melanics given here from intimate knowledge of the species concerned is very different from that conveyed by Ford (1964), who illustrates seven such species and says that one thing they have in common is that they rest fully exposed on tree trunks or rocks and that species that hide themselves in crevices are not involved. Not only is this incorrect; it is seriously misleading, as Porritt's observations make plain. Indeed one of the species illustrated by Ford – the Scalloped Hazel, *Odontopera bidentata* – while easily trapped at night, is usually extremely well concealed by day and is notoriously difficult to find. In an extensive study Bishop *et al.* (1978a, 1978b) found only one adult in the wild – in a crevice!

Although much disputed, while *B. betularia* does sometimes sit on tree trunks, it certainly prefers the under side of lateral branches, and some rest elsewhere. As this has a bearing on subsequent considerations, it is important to appreciate that while little has been recorded about the resting sites chosen by this species other than by individuals released under unnatural circumstances, Howlett and Majerus (1987) declared that "it seems certain that most *B. betularia* rest where they are well hidden", and that they were "convinced that exposed areas of tree trunks are not an important resting site for any form of *B. betularia*". As arguments relating to predation by birds have largely concentrated on this species it deserves to be emphasised that Porritt, who was familiar with the habits of many species, presented other evidence which throws doubt on the role of birds as significant predators. The curious case of the Grey Chi, *Antitype* (then *Polia*) *chi* (Noctuidae) is a striking example. This species showed "a gradual darkening from almost white to dark slate colour", the local distribution of which was remarkable. In the town and surrounding villages melanic individuals rested commonly on soot-blackened walls, yet "on the equally

black or even blacker walls bordering our high moors only half a dozen or so miles away, almost all the specimens are of the palest form and can readily be seen from a considerable distance." This he found at odds with protective resemblance. He also noted that some moths spend the daylight hours sitting conspicuously in view and that, if noticed early in the day, the entomologist can with confidence expect that individual to be in the same place if he returns there later – an observation which the writer has tested and can confirm. He concluded that while in smoky environments where a soot-covered background rendered them inconspicuous to enemies, natural selection may indeed favour melanic forms, the exceptions were so numerous that the theory could not be supported as a complete answer to the question of the biological significance of industrial melanism, or of melanism as such. Indeed the curious case of the Water Carpet, *Lampropteryx* (then *Cidaria*) *suffumata* seemed directly to contradict it. Of this geometrid the dark ab. *piceata* was fairly common in Scotland and might have been expected to be even commoner in soot-blackened West Yorkshire. But it was not. He knew of the finding of only one such individual there. Indeed he cited how Morley (1906) had demonstrated that over a seven year period it had become *lighter* in colour at Skelmanthorpe! That this moth should behave in a way so contrary to expectations is a problem that demands explanation by those who have sought to assess the significance of melanism. It is ironical – or apt – that an aberration of this species had even then been named *porrittii* – and is a very pale form! Moreover, Morley's paper on the then current variability of moths around Skelmanthorpe, where he lived, revealed further complexities. He noted that the results "are such that one need scarcely be surprised at any strange variation that may develop" and that "Not only is the melanic tendency remarkably well developed in many species locally, but of recent years other species not affected by melanism, are actually showing a strong tendency to vary in the opposite direction, and frequently examples are obtained, the bright colours of which are surprising". He then added that, as in *Lampropteryx suffumata*, "a few species...seem to be gradually leaving their darker hues, consequently the predominating forms are much lighter than formerly". That such a situation prevailed is seldom appreciated. The general perception is of a tide of melanism that swept through industrial areas and turned many species of moths black. This is misleading and hampers understanding of the biological situation that prevailed at that time, and of events that subsequently took place. Matters have not been helped by concentration on the Peppered Moth that has received an enormous amount of attention – probably more than that devoted to all other species combined – which has given an unbalanced, and sometimes erroneous, impression of a complex series of events.

LATER WORK, AND SOME ASPECTS OF THE WIDER SCENE

In the century and more that has elapsed since Porritt presented his paper, which he illustrated by use of a large number of specimens, and was discussed by several eminent biologists, the phenomenon of industrial melanism has been much debated, and experiments have been carried out. The complexity of the arguments and the huge volume of the work involved are impossible to summarise here, nor is this necessary. Suffice it to say that Porritt and his co-workers were not only privileged to be witnesses of ecological and evolutionary events in a way that is granted to few, but, to his credit, he recognised this and recorded what he saw. His observations, however, have not received the recognition they deserve, and some of the problems that they raise have not been appreciated, much less resolved. For example, the increased incidence and spread of pale individuals of several species, that followed a trend entirely contrary to the contemporary spread of melanism, seems not to have been considered, much less explained, and his findings have been almost universally overlooked. Although Robinson (1971) cites his 1907 paper, he makes no reference to the significant biological observations that he made on many species. E.B. Ford made no mention of this paper either in his book *Ecological Genetics* (1964 & subsequent editions) which deals extensively with the matter, or in his semi-popular *Moths* (1955), where he laments that collectors could "have obtained precise information on the rate at which the black forms spread and the conditions in which they

do so. In this they have consistently failed and our ignorance remains profound". Unknown to Ford, Porritt had done just that. He provided rather precise information on the rate at which several species became melanic. Ford referred to work by Gerschler in Germany on the increase in incidence of melanism in the Poplar Lutestring, *Tethea or*, a member of the Thyatiridae, but complained that, while it strongly suggests the magnitude of the change, it does so without the use of adequate sampling methods or accurate statistics, and went on to say that, had such been used, the story could have been a classic in evolutionary genetics. A more detailed picture emerges from Porritt's observations, which give an account of what took place in not just one but in *several* species.

From its increase in gene frequency from 1% to 99% or more in 50 years, Haldane calculated that the *carbonaria* form of *B. betularia* had an advantage of some 50% over the normal form in smoke-polluted areas. Ford calculated it in another way as 30%. Porritt showed that in *Colostegia multistrigaria* the rate of increase in the frequency of the gene for melanism was much greater than in *B. betularia*, which might imply an even greater selective advantage in the melanic form. Even more remarkable, he demonstrated that in the females of *Apocheima pilosaria* and *Agriopus marginaria* these attributes were acquired at a rate perhaps as much as ten times as fast as they were in *B. betularia* which was truly astounding. Whether Haldane's calculated advantage, and the even greater advantages implied for the species observed by Porritt, are real or are a deceptive by-product of the mechanism whereby melanism was acquired, is a vital issue to which we shall return. For all its lack of what is now called quantitative rigour, lamented by Ford when he considered the work of Gerschler, Porritt's account, more than a century ago, was sufficiently precise to demonstrate that a remarkable evolutionary event had taken place, and he illustrated this by reference to more than 40 species of moths that became melanic in South West Yorkshire within the experience of contemporary lepidopterists. Not only did he consider far more species than did the majority of observers, but he demonstrated that in some species the spread of melanism proceeded in different ways in the two sexes, i.e. it was sex-linked, and that the rate of increase of melanic individuals was greater in females than in males. This points to the operation of different genetic mechanisms in the two sexes.

These were remarkable findings by an amateur entomologist. Nor was Porritt reticent in expressing dissent when he believed that explanations suggested by others were at variance with what he believed to be the case. In particular he rejected what he believed to be facile interpretations of the role of predation, and recorded various anomalous situations that cast doubt on the universal application of a single explanation of the phenomenon of industrial melanism. Thus (Porritt 1926) he made the tantalising observation that one melanic form – the ab. *varleyata* of *Abraxas grossulariata* – was as rare in his area in 1906 as it was then, while, within less than 20 years of its appearance, the dark *nigrosparsata* form of the same species comprised almost 10% of the population. As all stages of this moth, melanic or otherwise, are distasteful to birds and mammals, and normal individuals display warning coloration, he could also have pointed out that there was no need to become inconspicuous. Indeed the reverse is the case, and it can hardly be argued that darkening confers protection – this species depends on being conspicuous to deter predators.

The significance of what Porritt recorded was made apparent when, half a century later, Kettlewell attempted to trace the history of industrial melanism in *B. betularia*. He suggested that the first record of a melanic individual in 1848 indicated an original mutation in c. 1810, from which a melanic element built up in the population to about 1%, at which it was likely to have been first noticed (in 1848), after which he postulated a more rapid increase in its incidence. After a gradual build up to c. 10% he suggested that its frequency might then have risen to 70% in from 10 to 15 years. He did not know whether all melanic individuals were derived from a solitary mutant or whether there were several such. Cook *et al.* (2004) mention that only "two or three" *carbonaria* were recorded during three decades of study in Siberia, where it is sometimes sufficiently abundant to defoliate

forests, so such mutants arise very rarely in non-industrial areas. Kettlewell's exercise was inevitably speculative, and throws into strong relief the more concrete nature of the observations of Porritt and his fellow entomologists who recorded the first appearance of the phenomenon in several species, and traced its much more rapid spread to its near universal manifestation in many such, in a restricted area, between about 1880 and 1906. If the history of melanism in *B. betularia* was anything like that suggested by Kettlewell, it is improbable that the melanism reported by Porritt in many species could have originated by random mutation and spread so quickly as a consequence of natural selection. The required intensity of selection was clearly far too great to be achieved so rapidly. Moreover, elements of the natural history of some of the species, that he also recorded, make crystal clear that natural selection was sometimes not involved at all. The profound implications of this startling fact are considered later.

Porritt continued to be interested in the significance of melanism throughout his life and was never convinced that it protected moths against the depredations of predatory birds. He was, for example, puzzled by the case of a noctuid, the Light Knot-Grass, *Acronicta menyanthidis*. This species was common in South West Yorkshire where, as he put it, "melanism is rampant", yet here it maintained a pale colour almost entirely. On the other hand, in areas near York and Selby, where there was little smoke, it occurred mainly as the melanic form (Porritt, 1919). This story he amplified when (Porritt, 1926) he reported from the experience of a local collector, the Rev. C.D. Ash, that, for as many years back as anything had been known of it, this species had been "so entirely of the black form" at Skipwith "that probably not two percent of the pale form are to be found there". What is highly significant in the present context is that *A. menyanthidis* spends the day resting on rocks, stones and, where they are available, fence posts and similar structures, where it is fully open to view. In clean areas, such as Skipwith, this is clearly *not* behaviour that hides the almost always melanic individuals that frequent the area, from birds, or any other visually hunting predator. On the contrary it renders them conspicuous. Such behaviour, and that exhibited by pale individuals of *Antitype chi* that Porritt recorded as resting on soot-blackened walls where they were very conspicuous, suggests that birds are not much interested in taking moths from surfaces on which they rest, apparently with impunity, fully exposed, by day.

Ironically, in the same paper Porritt (1926) was able to report that, until about five years earlier, when the first such was found, no melanic individual of *A. menyanthidis* had been seen on his local moors where this species was "almost invariably of the palest form we know in Britain". A few more had been found each year subsequently. This recent history he compared with that of the Common Heath, *Ematurga atomaria*, like which it was abundant and where the two species co-existed. *E. atomaria* had been gradually becoming melanic "for many years" and was by then predominantly so. This information is interesting in showing how *A. menyanthidis* began to become melanic about 40 years after several other species did so, and at least 70 years after *B. betularia* began to do so. Porritt's scepticism about the causes and significance of melanism in the Lepidoptera, based on his observations on a considerable number of species, can perhaps be summarised as a belief that no one explanation fits all cases, and that some species behaved in a manner that is entirely contrary to the generalisations that some have suggested. It is clear from his observations that to extrapolate from conclusions reached on the basis of work on the Peppered Moth – even if these are correct, which is often arguable – is unwise, and sometimes misleading.

The more one delves into the vast literature on industrial melanism in moths, the more impressive are Porritt's achievements revealed to be. He made observations on far more species that display such melanism (or appeared to react in other ways to the conditions that led to it) than did most of those who have considered the phenomenon, many of whom have concentrated on a single species, the Peppered Moth. Although the details were not then known he showed how, of the species that became melanic, not all did so by genetic means similar to those employed by *B. betularia*, in which, essentially, a dominant allele of

a single gene is responsible for the *carbonaria* form. (In some areas another allele, *insularia*, is responsible for a generally paler melanic form, but no such complications were involved in his home area.) Moreover he demonstrated that species which employ the same mechanism as *B. betularia* became melanic much more rapidly than that species – and that some of those that exploited a different mechanism became melanic up to perhaps ten times as fast. He showed that in some species the darkening was not immediately 'switched on', but developed gradually over several generations and, even more striking, that in some species, while females employed a mechanism akin to that of the Peppered Moth, the males became melanic gradually, and did not even begin to display this phenomenon until full melanism was well established among the females. He also showed that, while many species became melanic in an industrial area, others, with which they co-existed, reacted in an entirely contrary manner and became paler.

WAS INDUSTRIAL MELANISM AN ADAPTATION TO PROTECT MOTHS AGAINST PREDATION BY BIRDS IN A CHANGING ENVIRONMENT?

That moths are eaten regularly by birds and that, by rendering them less conspicuous in soot-blackened areas, melanism offers protection against such predation is a scientifically respectable hypothesis. It has been accepted by many who have considered the matter that this is so. This depends on two simple assumptions being correct – that birds commonly eat moths, and that in areas with a soot-blackened background they prey differentially on light-coloured individuals. As Porritt was quick to point out, however, some of the species that became melanic spend the daylight hours in situations where they are very well hidden from birds. From the standpoint of protection, it is entirely irrelevant whether they are camouflaged or highly conspicuous. The acquisition of melanism by these species was definitely *not* a means by which they became cryptic and thereby escaped the attention of insect-eating birds These simple facts, ascertained by Porritt, reveal that two widely held assumptions on which the establishment and spread of industrial melanism are based, are, certainly in many cases, invalid. Moreover, the rapidity with which melanism spread through the population of some species implied not merely very efficient removal of typicals but a mutation rate far higher than that which normally pertains in nature. Also completely contradictory were the observations of Porritt and Morley that, as the background became darker, some species gradually became *paler* in colour. That very pale individuals of *Antitype chi* should sit throughout the day on soot-blackened walls where they were very conspicuous, and should therefore have been easily seen by birds, and the similar anomaly that the pale form of *Acronicta menyanthidis*, which rests openly in view, should be common in South West Yorkshire but was represented almost entirely by the melanic form in clean areas to the east, he also found difficult to equate with an assumed need to avoid the attention of predatory birds, as indeed it is. Such facts challenge the interpretation of industrial melanism and upset long held beliefs with which they are incompatible. I have also yet to locate a record of *B. betularia* (other than those liberated or deliberately displayed) being taken by a bird in the wild, which must be a rare event, if it happens at all.

Porritt knew that larval lepidopterans are eaten in vast numbers by birds of many species but found no reason to suppose that adults were subjected to any comparable hazard. He did *not* deny that some species merge effectively with their background when settled, and that some of those that rest on rocks and walls are well camouflaged, at least to human vision, which must have been part of the evidence that caused him to believe that birds seldom pick moths from surfaces. Such assessments are now complicated by the knowledge that human vision differs from that of birds in its perception of both colour and luminance, and rock-hugging species may be camouflaged as protection against such predators as lizards, which are abundant in warmer climates, and run over such surfaces. Such camouflage may have been more important in times past.

He was also aware that, as well as those allegedly protected against predation by being melanic, many, indeed most, other moths remain hidden by day. A well known example is

the Old Lady, *Mormo maura*, a large, dark brown noctuid of which several individuals may roost together in dark situations. These have even been known to 'home' to their roost on several consecutive days after their nocturnal excursions. Related species, such as the Mouse Moth *Amphipyra trogopoginis* and the Copper Underwing *A. pyramidea* have similar habits, and the Brindled Ochre *Dasypolia templi* hides under stones by day and females even hibernate there throughout the winter. *D. templi*, long thought to be largely confined to the Huddersfield area, was much studied there and revealed much about its habits (Brooke, 2007). Long-lived adult females must seldom, if ever, encounter a bird that takes insects from the ground. These and many other species are simply hiding from light. They are negatively phototactic, as are many nocturnal animals of diverse affinities, and the reactions they display automatically put them out of reach of most diurnal predators. So far as protection from enemies is concerned, their colour is entirely irrelevant. A few species, if inadvertently disturbed by day, can distract an enemy by 'flashing' coloured hind wings, which grants time in which to 'disappear' again.

The behaviour of many other moths casts doubt on the hypothesis that industrial melanism was an agent of camouflage. If they are eaten by birds, and if settled individuals benefit from camouflage, it is difficult to appreciate how non-camouflaged, even conspicuous, species cope with this alleged hazard when they draw attention to themselves by flying, in some cases not particularly strongly, by day. Examples include the Speckled Yellow, *Pseudopanthera macularia*, Chimney Sweeper, *Odezia atrata*, Common Heath, *Ematurga atomaria* (which became melanic in Porritt's area), and Mother Shipton, *Callostege mi*, all of which are easy to see, and slow-flying. Moreover the first three are often gregarious, which means that a search image can easily be established, and it is not difficult to imagine even a small bird catching them easily – but they seem not to be molested. Moreover, although predominantly nocturnal, even in Britain there is a diverse array of diurnal moths. Some are distasteful, and display aposematic coloration, and such skilled flyers as the Humming-bird Hawk, *Macroglossum stellatarum* and the two Bee Hawks, *Hemaris* spp. are probably difficult to catch. Others enjoy no such protection. Some are conspicuous, others, such as the Silver Y, *Autographa gamma*, and Antler Moth, *Cerapteryx graminis,* are sometimes abundant. 'Microlepidopterans' provide other examples. Many species are completely concealed, sometimes in vast numbers, by day, often among dense vegetation; others fly openly in sunshine. Like many of its congeners the tortricid *Cydia nigricans*, a well known pest of peas, flies in sunshine in the afternoon. Other species of *Cydia* hide by day and fly at sunset. Such facts support Porritt's contention that adult moths are seldom picked from surfaces by birds – a view that he consistently held. He did not say that birds never take moths: only that predation was demonstrably insignificant in many species, and that some of those that became melanic appear to be completely immune from predation by birds. One moth that is eaten (essentially males only) by birds is the Northern Eggar, *Lasiocampa quercus callunae,* which I have seen persistently hawked by a Merlin – which feeds predominantly on small birds – which also catches male Emperor Moths, but the number of Merlins is so few that such predation is probably inconsequential. It is also relevant that while butterflies are sometimes attacked by birds, and occasionally bear beak marks as evidence of their ability to escape, and some indeed fall prey to birds, there is little to suggest that they suffer much mortality as a result. Certainly in Europe one can see many butterflies flying in open spaces completely free from molestation, and I have never seen a bird show interest in aggregations of any of the various species of which males in particular have congregated to imbibe moisture from wet ground. Tropical butterflies are certainly taken by birds, and distasteful species have evolved that are mimicked by edible species, but these phenomena, which reflect the vastly more diverse faunas of both butterflies and birds in tropical than in temperate regions, have no parallels in Europe, and the well-known case of the distasteful North American Monarch butterfly has no counterpart here.

Such facts indicate that the idea that melanism in moths grants protection against predators, especially birds, fails as a general explanation because it ignores their diversity

of habits and behaviour. Even though it seeks to impose a explanation on only a restricted sub-set of species, these display sufficient diversity to refute it. They remind us that moths owe much of their success to their diversity of habits and ways of life. It is impossible to generalise, but among species that became melanic during the industrial era, in several cases this was certainly not a means of providing concealment from predatory birds.

A vast amount of information on the food of birds is provided in *The Birds of the Western Palearctic*, (BWP) but, inevitably, in various ways and at levels of detail that differ much between species. No detailed search has been made but the general impression given is that adult moths seldom feature greatly in the diet of diurnal birds. Information on the Tree Creeper, which feeds much on tree trunks, is disappointing. Comments such as "less than 3% larval Lepidoptera", "small numbers...(chiefly larvae)" and, on items fed to young, "Lepidoptera 6.7%" – presumably larvae? do no more than suggest that adult moths are not much eaten. Likewise information on the trunk-frequenting Nuthatch is vague. Apart from those fed to young – almost certainly larvae – Lepidoptera seem not to be of much importance. To nine warblers – Blackcap, Cetti's, Reed, Sedge, Wood, Chiff Chaff, Willow, Grasshopper, and Lesser Whitethroat, adult Lepidoptera are of negligible importance, but larvae are often eaten. In the stomach of one Willow Warbler a Russian study found 11.4% "adult Lepidoptera", but this is in contrast to many references to larvae only; e.g. in two studies 20% of 571 items and 16% of 801 items were larval lepidopterans, but no adults were present. The Spotted Flycatcher, which takes more than half its food in flight, is opportunistic. Of 2743 victims, 66.2% were Diptera, 31.1% beetles, ichneumons and aphids, and 'others' 2.7%. However, in Eastern Europe, where *Lymantria monacha* was "especially numerous", of 418 identified items, 38% were of this moth, which is intriguing as it is nocturnal and rests by day on tree trunks. The Spotted Flycatcher is anything but a trunk-searcher. The moths may have settled elsewhere. In Germany, *Tortrix viridana* comprised 31.6% by number of items fed to young, with 30% 'Lepidoptera' – adult or young? The feeding of Titmice is mentioned in the next section.

SOME ASPECTS OF THE BIOLOGY OF *BISTON BETULARIA* AND THEIR RELEVANCE TO THE ROLE OF MELANISM

By far the most studied species associated with industrial melanism is the Peppered Moth, *Biston betularia*. In spite of this some very relevant aspects of its life cycle appear to have been largely ignored. First, it is important to appreciate that, as Cook (2003) has pointed out, the average life span of an adult in nature is little more than a day. Adults do not feed. As there is one generation a year, between them, the egg, larval and pupal stages are exposed to the hazards of life, and to natural selection, for some 300 times as long as the adult. Earlier workers cited somewhat longer – but still very brief – adult life spans. Thus Bishop (1972) noted that mating takes place within half a day after emergence and that females lay eggs within two days of doing so, while Mani (1990) referred to a life expectancy of "around 3-4 days", and in some very abstruse calculations used two days as the mean time interval between emergence and egg-laying. In accepting Cook's more recent estimate it may be noted that, even if this is doubled, selection operates on the early stages for 150 or more times as long as on the adult. Furthermore selection seems likely to be most intense, and is certainly more prolonged, on the larvae, which are variable in colour and, like many lepidopteran larvae, are presumably vulnerable to predation, especially by birds, and predatory insects, and to the attacks of hymenopteran parasitoids such as ichneumons. Females usually mate only once but Liebert and Brakefield (1987) reported that of 116 females, almost 10% did so twice or three time. Of the four that mated thrice, two were kept alive but never laid eggs after the event, though dissection showed that eggs were present. Males can mate more than once. Melanism conceivably affects mate preferences, but mating often begins in the dark. It is impossible to know exactly what effect, if any, the alleles of the gene for adult melanism have on early stages of the life cycle. What is known, however, is that they can be correlated with the viability of the early stages as a whole. To this we shall return.

After dark newly emerged males disperse to all points of the compass and, as Bishop (1972) showed, fly up to 5 km. in search of females that attract them by scent. Others have shown that they sometimes fly even further than this. Even if adults are eaten by birds on the day following the first night's activities, half of them will presumably be males – figures are needed – which, having usually mated on their first, and perhaps only, excursion, are expendable. They have already passed on their genes. Having done so, their loss is of no evolutionary significance. Whether or not they are melanic is by this time irrelevant. Thus up to half of any such predation will have no effect on the composition of the next generation. Selection for melanic or typical individuals must therefore be restricted almost entirely to that on the females before they have deposited their eggs. After oviposition, to be taken by a bird is of no significance to future generations. Any selection by a predator at this stage is nullified by the biology of the moth. As probably no more than half of the victims (if any) of predation by birds will still influence the genetic composition of the next generation, this will retard the effects of any selective predation on adults. The effect of such predation is likely to be smaller than an estimate uninformed by knowledge of the natural history of the moth might suppose. It is a less effective means of influencing adult coloration than it might appear to be at first sight. Because of the short period of time that unmated adults are exposed in daylight, the risk of predation is small. The role of selective predation in the spread of melanism in *B. betularia* is therefore at least diminished. Indeed, that selective predation need not be involved at all in the acquisition of melanism is categorically demonstrated by other species that, never exposed by day, encounter no such predators, yet not only became melanic in the same area as did *B. betularia*, but did so even more rapidly. All these caveats assume that birds take this species in nature. In fact, while large numbers have been offered to birds, the taking of truly wild individuals appears not to have been witnessed.

Much work on *B. betularia* has been aimed at ascertaining to what extent adults are eaten by birds, and whether melanism improved the match between moth and background in soot-blackened areas, and therefore granted a measure of protection against such predators. Typical individuals harmonise well with clean, but not with soot-blackened, tree trunks – but see Harrison (1956) – and many experiments have been carried out by exposing this species, put down, alive or dead, on tree trunks. However, these are not the most favoured sites. Clarke *et al.* (1985) worked on this moth for 25 years and saw only one individual on a tree trunk, and one on a wall. Mikkola's (1984) experiments indicated that they prefer the underside of branches – he gives a photograph – and the observations of Liebert and Brakefield (1987) and Majerus (1998, 2007, 2009) suggested that they particularly favour the joint where they arise. It is not a good tactic for all individuals to settle in the same sort of well-defined site. Some may of course settle in unsuspected places elsewhere. Particularly striking is that, contrary to earlier experiments which had various limitations, Mikkola, like several others, found that neither typical nor *carbonaria* showed any difference in their choice between blackish and whitish backgrounds - which one might have expected them to make had harmonising with the background been their objective.

All experiments that expose moths to birds are inherently flawed, for a simple reason that has never been appreciated. The results are entirely predictable. Moths displayed on a background that renders them conspicuous will be taken more frequently than those displayed on a background against which they are inconspicuous. This simply confirms the obvious. Only if they gave results that differ from this prediction would they be informative of a situation that demands attention. This point, an element of a revised analysis of the history of industrial melanism, put forward towards the end of this paper, should be borne in mind whenever such experiments are mentioned.

A lack of information on just where *B. betularia* settles had long been a great lacuna in our knowledge. Majerus (2007), however, located 135 individuals resting in what he believed to be freely chosen sites. His much greater success than Clarke *et al.* in locating settled individuals reflects the fact that these were not 'wild' moths that had emerged in nature, but had been reared, and released in specific areas. Nevertheless, although not free

from bias, they provide useful indications of the kind of site preferred. Some 50.4% were on lateral branches of trees, and of these 89% were on the lower half of the branch. A further 37% were on tree trunks. Earlier experiments by Kettlewell had been criticised because he released moths (in large numbers) onto tree trunks. Although Majerus suggested that his findings go some way to justifying Kettlewell's methodology, 63% of the more naturally chosen sites were not tree trunks. He also forgot that, with Howlett, he had earlier been "convinced that exposed areas of tree trunks are not an important resting site" for this species (Howlett & Majerus 1987). A further 12.6% settled under or among twigs. It is also possible that some settled too high in trees to be detected. Indeed, by the very nature of the observations there is no means of proving that the moths did not use sites other than trees. Absence of evidence is not evidence of absence. In nature, males often disperse for several kilometres after emerging so the results of Majerus were clearly atypical. The preferences shown, while informative, are inevitably overestimates. One also wonders why resting *B. betularia* are so seldom seen in nature. The brevity of the adult life span, especially of males, is one obvious reason. Another is the lower density of the moths in nature even than in cases where they were liberated in modest numbers, as by Majerus – which is relevant to the search image of potential avian predators. Birds will eat these moths, but so seldom encounter them that their depredations are probably inconsequential. The only convincing evidence of their relevance in this respect would be records of the frequent taking of this species by birds in nature.

It had long been thought, as did Porritt, that birds were not significant predators on moths, and whether they sought them selectively had received no attention. The experiments of Kettlewell, who pioneered investigations into the matter, using *B. betularia* as test material, who deserves credit for this, are now famous, or notorious, according to one's interpretation. Before undertaking work in the field he made observations in an aviary where he exposed *B. betularia* to a pair of Great Tits, which had young there. Their behaviour on first encountering the moths was enlightening (Kettlewell 1973). For the first two hours of the first day they "did not recognise either form [typical or *carbonaria*] of *B.betularia* as an article of diet". These and other observations "suggested that it was necessary for Great Tits to have a period of contact with their prey before recognition". This suggests that *B. betularia*, which is often sparsely distributed, is not likely often to present a recognisable search image for Great Tits (and other birds?). In nature the Great Tit takes many lepidopteran larvae and eggs (see BWP) but otherwise seldom takes insects more than 1cm in length. Of 2552 insects of all kinds taken in English woodland, 68% were < 6mm in length. The Blue Tit, a vast consumer of lepidopteran larvae, otherwise takes even smaller prey. Of 6507 insects from stomachs in south west England 58.7% were < 2mm in length, and only 9% exceeded 6mm.

Held up by Ford as "a model for such field work in the future", in hindsight Kettlewell's experiments can be seen to have been seriously flawed. Using adults that emerged from a large stock of pupae, he liberated 584 Peppered Moths – some *carbonaria,* some typical – in a wood near the industrial centre of Birmingham, and 969 in a heavily lichened wood in pollution-free Dorset. About 50 individuals of each phenotype were liberated at the same time onto tree trunks and, in Dorset, watched from hides to see if they were eaten by birds, which some were, and were replaced when all individuals of one phenotype had disappeared. In traps set to catch survivors the percentage of melanics caught in Birmingham was approximately twice that of typicals: in Dorset the percentages were reversed, demonstrating greater survival of melanics in Birmingham and of typicals in Dorset – exactly as one would predict. In Dorset five species of birds were seen to prey on the conspicuous melanics. Although their predictability went unnoticed, these clear-cut results were criticised by those who rightly pointed out that the moths were available at far greater densities than is the case in nature. Just how much denser has probably not always been appreciated, nor is it evident from much of the literature. Based on light trapping, which catches essentially only males, which are attracted to more or less sedentary females by scent, the number per square kilometre in the Wirral and North Wales was estimated as

7.3 and 22.3 respectively. Assuming equality of the sexes Bishop (1972) rounded the higher of these figures to 44 individuals per km^2. The sparsity of *B. betularia* at these sites is put into perspective by comparing it with estimates of the population density of *Odontopera bidentata* at several sites in the Manchester and Liverpool areas. As Bishop *et al.* (1978b), who provide tables of data, record, populations of the latter could be "up to 2000 times more dense than those of the Peppered moth". In one small area, on each night of his experiment Kettlewell released more moths than are present in 2 km^2 of the richer of the two surveyed sites. Here the density was less than one individual per 20,000 m^2, yet Kettlewell liberated batches of 100 moths in one small area, *and* replaced them as they fell victim to predators or disappeared. Under such conditions, birds that had probably never previously encountered a Peppered Moth would be attracted. The situation has been aptly compared to a continuously replenished bird table, and clearly bears no relation to natural conditions.

Subsequent releases of 218 *carbonaria* and typical individuals at Birmingham gave similar results. The anomalous nature of the experiment is brought home by the fact that a pair of Redstarts, attracted by the cornucopia of food, caught at least 58 moths during two days of observations! Typical and *carbonaria* forms were released in equal numbers and, predictably, a greater number of the more conspicuous typicals was taken by the Redstarts. That birds will eat settled individuals of the Peppered Moth was shown but, as Cook (2003) points out, at the low densities at which it often occurs in nature, predators are unlikely to become familiar with it as a food source. There appear to be no records of truly wild individuals taken by birds.

THE ENIGMATIC REACTIONS OF *BISTON BETULARIA* AND OTHER SPECIES TO ENVIRONMENTAL CHANGES

Beginning some time after 1848, the Peppered Moth population in South West Yorkshire gradually became melanic, and by the turn of the century was almost entirely so. This change was generally accepted as an adaptation which, by matching the blackening of the environment that accompanied the soot- and smoke-producing industrial era, rendered it (and other species), inconspicuous to predatory birds, and this is still a key element in the orthodox story of industrial melanism. However, in 1904 Porritt drew attention to a development that was difficult to reconcile with this interpretation. He reported that the melanic form of this moth had not only "now almost eliminated the ordinary pale form in the South West Riding" – where soot-blackened conditions prevailed – "but bids fair to do so throughout the county at no distant date". It was extending its range beyond the industrial area and not only spreading into uncontaminated countryside but replacing the typical form there. As the melanic form was surviving in increasing numbers *outside* soot-blackened areas, where its dark coloration clearly did *not* provide camouflage, it was obvious that this did not prevent colonisation of localities where the alleged advantage of concealment from predators did not apply. Here, indeed, it was more conspicuous than the pale form, and more vulnerable to the alleged danger of predation, which was embarrassing for those who claimed that it conferred protection in the industrial area. To Porritt this must have been self-evident. His prediction of further spread of the melanic form was amply fulfilled. Such individuals eventually greatly outnumbered the typical form in many 'clean' areas both in Yorkshire and elsewhere, not just as minor incursions but over extensive regions. Indeed by the late 1960s it was estimated that probably over 95% of the Yorkshire population was melanic and that this species was "generally distributed and often common there" (YNU, 1967-1970). Similar anomalous situations were reported elsewhere by various authors, who referred to the melanic form as then being at a 'cryptic disadvantage'. This dramatic new development, extending as it did over an enormous area, is completely at odds with the idea that the melanic form had largely replaced the typical form in soot-blackened areas because it harmonised with the background and that its success was the result of differential predation by birds which selectively removed pale rather than melanic individuals. On the contrary, it indicated that birds were not much concerned with taking

moths from surfaces, and that if they did so they were singularly ineffective in taking melanic Peppered Moths from pale backgrounds where they were more conspicuous than the typical form. Indeed melanics gradually replaced the pale form just as they had in places where the advantage of matching the background lay with the melanic form! It could hardly be argued that differential selection of prey by birds, based on a match or mismatch with the background, applied to dark but not to light backgrounds. An out and out sceptic could argue, with considerable justification, that the new situation destroyed the original hypothesis, which is equally inapplicable to cases of pale forms of other species resting openly in industrial areas and dark forms doing likewise in clean areas.

That melanic *B. betularia* became so widespread and constituted such a high proportion of the population in rural areas deserves emphasis as these facts and their significance seem to have been underestimated. Even Cook and Turner (2008), two highly competent investigators, refer to such areas as "less affected regions" where melanics "arrived by migration", and add that "Although these places sometimes offered conditions favourable to persistence of a low frequency of melanics, a threshold degree and extent of pollution appears to have been required". In fact melanics overwhelmingly predominated in rural Yorkshire. That this was so is not helpful to the belief that birds selectively prey on individuals that do not match their background. Moreover, melanic forms of other species followed the same pattern as *B. betularia* and colonised large tracts of unpolluted countryside, records of the Engrailed, *Ectropis bistortata*, mentioned by Porritt (1904), being early examples of a more widespread phenomenon in Yorkshire.

Long after Porritt had drawn attention to the extension of range of melanic Peppered Moths beyond soot-blackened industrial areas, Ford (1937) suggested that the melanic form increased in industrial regions primarily as a result of selection for characters other than colour, and that one of the effects of genes for producing melanism may sometimes be to confer a physiological advantage. Others had already suggested that melanic forms of other species were hardier than typicals. He suggested that this advantage may have been offset under normal circumstances by the handicap of black coloration which rendered its possessor conspicuous, but that this was not a drawback in industrial areas. By 1955 however, he had decided that melanism was in fact an asset to *B. betularia* in industrial areas, but not a necessity. He also referred to the spread of the melanic form into clean countryside, and speculated that the melanic populations in industrial areas provided a "suddenly acquired...numerically vast reserve" from which to invade such areas, and that this probably gave it "a chance to evolve rapidly and improve its physiological advantages" – a remarkable claim that was not explained. He then noted that it had always been accepted that birds were the only predators that could selectively eliminate melanic moths in unpolluted, and pale moths in polluted, areas, but that this was only then being confirmed by the work of Kettlewell, then in progress. Still later (Ford, 1964), as a result of how that work was then interpreted, he had changed his views again and conceded that he had attributed "much too little importance to the selective effect of predation in manufacturing areas". Ironically the evidence for such predation is highly questionable. It is certainly absolutely inapplicable to certain other species. He also conceded that he had "certainly attached too much relative importance to the greater viability of the successful melanics", but maintained that such was acquired later, and went on to say that his theory to account for industrial melanism, "assumed heavy elimination by predators", of individuals which match their background least well – which inlcudes melanics in clean areas! Porritt would wonder how this could operate in secretive species that are undoubtedly exempt from any such predation. Ford then credited Kettlewell with providing the necessary information – by pioneer experiments that were in fact seriously flawed. He also accepted his alleged demonstration that moths take up positions in which their colouring matches their background, which, although also claimed by others, has been shown repeatedly to be erroneous. Thus Ford held three very different views in less than 30 years, of which the most recent appears to be based on an erroneous assumption.

It is not easy to reconcile Ford's changing views with the spread of melanic

B. betularia into rural areas. His early assumption was that they enjoyed enhanced viability ('superior hardiness') that was more than sufficient to compensate for the loss of cryptic coloration – in whose importance, however, he believed in 1955 – but in 1964 he conceded that he had attached too much importance to this assumption. But, what use is enhanced viability if being black increases the chance of being eaten? The spread also revealed the ineffectiveness of selective predation, the prime importance of which he was now at pains to emphasise. To claim enhanced viability for the colonising melanics also inevitably weakened the case for their survival in soot-blackened areas as a consequence of differential predation. If they enjoyed greater viability than non-melanics, they could expect to survive better for this reason alone in such situations. There was no need to invoke differential predation, though this was not ruled out. To claim that melanics were able to spread into clean areas because of enhanced viability is inevitably to concede that selective predation – the raison d'être of all arguments and experiments – was ineffectual – as the facts showed that it was. No coherent argument emerges. Others later claimed to have provided evidence of enhanced viability. Thus Lees and Creed (1975) estimated that in similarly colonised clean East Anglia, non-*carbonaria* individuals were at a physiological disadvantage of up to 30%. Their calculations and arguments, based in part on observations made elsewhere by Bishop, are unconvincing and, as we shall see, the alleged physiological disadvantage of non-melanics did not prevent them from subsequently ousting the melanics.

In order to analyse this matter it is necessary first to consider that Creed *et al.* (1980) sought to establish the pre-adult viability of the genotypes associated with melanism in *B. betularia*. This they did on the basis of crosses recorded in the literature and their own data, the alleles concerned being 'typical', '*insularia*' and '*carbonaria*'. The data were hedged by caveats, but CC – the *carbonaria* homozygote – was clearly the most viable genotype. Although (provided one ignores the fact that many other, unstudied, genes might affect viability) this explained the preponderance of melanic adult moths offered to the environment for selection in industrial Yorkshire and in clean East Anglia, it had nothing to say about the effects of selection on adults, which operates during a very small fraction of the life cycle and would need to be extremely intense and adverse to reverse any alleged enhanced viability of the CC genotype passed on by the pre-adult stages. It is important to appreciate that we are concerned with an organism that has four separate, and very different, ecologies. The viability of the early stages calculated by Creed *et al.* (1980) was not necessarily the same as that of the adult moth, whose structure, life-style, and role are utterly different from those of earlier stages. It had nothing to do with the selection of adults in soot-blackened – or clean – situations. If there was a preponderance of melanic adults, unless selection against melanism was intense, most of the offspring would inevitably have melanic genotypes, i.e. genotypes that gave rise to melanic adults.

Particularly damaging to the belief that differential predation matched moth to background was that melanic forms of species other than *B. betularia* also spread into the clean areas of Yorkshire. These included the Scalloped Hazel, *Odontopera bidentata* and the Clouded-bordered Brindle, *Apamea crenata* (known to Porritt as *Xylophasia rurea*) that he had recorded as having become melanic in smoke- and soot-blackened South West Yorkshire in his account of 1907. Melanic individuals of *O. bidentata* remained common in some unpolluted areas in the late 1960s (YNU, 1967-1970) and were still present, but in decline, near York in the 1990s and early 21st century (Cook *et al.*, 2005), and melanic *A. crenata* were still to be found near York in 2004. It would be stretching credulity to suggest that the melanic forms of these, and other species, also enjoyed enhanced viability. It can however, be argued with considerable confidence that their spread into clean areas effectively destroyed the claim that the melanic forms of these and other species were selected by differential predation by birds to match them to their background. This was clearly not the case. As reported subsequently, *O. bidentata*, which leads a cryptic existence, must seldom or never be exposed to bird predation, and was not even preyed upon selectively when offered to birds in experiments.

Following earlier restrictions on smoke emissions, the implementation of Clean Air Acts in 1956 and 1968, a decline in manufacturing industries, and the increasing use of less polluting fuels than coal, conditions in areas where industrial melanism was most apparent have ameliorated, soot-blackening has been reduced, and the environment has become much cleaner. Moreover, the incidence of melanism in moths has declined. This is best documented for the Peppered Moth in which the incidence of melanism has been followed in some areas, in both directions, for many years. Particularly relevant to the situation in Yorkshire, Cook *et al.* (2005) have presented information on the number of individuals of this species and of *Odontopera bidentata* captured in a mercury vapour light trap near Leeds from 1967 to 2003, and of *Apamea crenata* from 1970 to 2003. Of the Peppered Moth, in which for the early years of the observations the vast majority of individuals were melanic, as they were known to be before that, non- melanics eventually preponderated for the first time in 1994 and, apart from 1996 and 1997 when the samples were too small to be significant, have done so ever since. In essence melanics predominated in *O. bidentata* until 1990 then yielded to non-melanics. In *A. crenata*, after many years of melanic domination, non-melanics predominated in 1993 and the following two years, since when the situation remained in a state of flux until 2003. One interpretation of these facts is that during the period that the background became dark as the result of pollution, a darkening of the moth conferred an advantage by making it less conspicuous to predators, and dark individuals enjoyed a selective advantage; whereas when the background became lighter in colour the advantage passed to less dark individuals. To some it is perverse to think otherwise. The same logic is applied to other species that display a similar trend. However, this apparently self-evident correlation is open to challenge.

If, during the years of high levels of pollution, melanic individuals enjoyed superior viability in industrial areas, where they were also favoured by selection on the basis of matching the background, survival would be favoured on both counts. However, supposed superior viability of melanics had unfortunate implications for other elements of the argument. In clean regions colonised from industrial areas, melanics lost whatever advantage was conferred by matching the background, but, according to some, in the case of *B. betularia*, enjoyed greater viability than non-melanics, and for long flourished there. Indeed they fulfilled Porritt's prediction of 1904 and, more than 60 years later, had almost eliminated the pale form throughout the whole of Yorkshire. Being melanic was clearly not greatly disadvantageous in clean, unpolluted countryside. The same is true of other species such as *O. bidentata* and *A. crenata*, melanic forms of which likewise colonised such countryside. This being the case, why then did melanics subsequently yield to the allegedly less hardy typical form in these areas as, apparently inexplicably, they did? There were no obvious associated environmental changes. And why, if they enjoyed greater viability than such individuals, did they also yield to non-melanics in former soot-blackened areas that became clean?

An enormous increase in the incidence of melanics in areas such as South West Yorkshire during the industrial era, and their subsequent decline when conditions became cleaner, suggested the selection of adaptive traits. A similar great increase in the incidence of melanics in unpolluted regions, where over large areas they largely ousted non-melanics did *not*. Their subsequent decline there, unaccompanied by any obvious environmental change, is difficult to understand, particularly if the *carbonaria* alleles of pre-adult stages of *B. betularia* are associated with enhanced viability as they have been alleged to be. Indeed, what the eventual replacement of melanics by the typical form in unpolluted areas certainly did, was to refute the claimed difference in viability of the two morphs. If the typical form was in fact at a physiological disadvantage of up to 30%, it could hardly have ousted the melanic form, to which it had indeed just ceded predominance after a long reign as the undisputed characteristic genotype of the area. An inadvertent experiment, better than any that could have been set up by would-be investigators, exploded that myth. Why the melanic form was able to expand into, and predominate in, clean areas remains to be explained. It can hardly be argued that differential selection of prey based on a match or

mismatch with the background applied to dark, but not to light backgrounds. Indeed, one thing that this series of changes clearly demonstrated was that the idea of being, or not being, melanic was related to protecting individuals against attacks by birds by matching moth to background, was a weak hypothesis. In clean areas melanism rendered its possessors conspicuous. As Berry (1990) conceded even before these matters had become so obvious, "the maintenance of melanic frequency is now perceived to be less dependent on bird predation" than formerly supposed. The facts suggest, as does the enormous diversity of colours and wing patterns exhibited by nocturnal moths, that if they remain still by day, sometimes hidden to various degrees, their coloration and colour pattern are of scant concern in relation to predation. These attributes are related to other aspects of their biology.

In a nutshell: melanics first ousted non-melanics from polluted then, surprisingly, from unpolluted countryside. They evidently enjoyed some advantage in *both* environments. At the present time, they are being ousted from *both* environments by the form over which, very recently, they overwhelmingly came to predominate in both. No convincing explanation has yet been provided, but certainly differential predation by birds is no answer. If the form that did not harmonise with the background was selected as prey to a significant extent, the melanic form should never have ousted the non-melanic in clean areas. To argue that this was due to reduced viability of the pale form does *not* explain how this so encumbered form was able to oust the allegedly more viable melanic under any circumstances, including those prevailing in clean areas in which its alleged reduced viability had led to its virtual elimination by melanics not much earlier!

SOME UNCERTAINTIES ABOUT PREDATION AND MELANISM

The work of Lees and Creed (1975) exemplifies the sort of investigations that have been made in order to elucidate the importance of predation on moths, and the role of melanism in modifying it. As did most investigators, they used dead moths, killed with ethyl acetate after emerging from bred stock, and subsequently deep-frozen after being arranged in a life-like resting posture. These were affixed to tree trunks. In East Anglian woods, Wrens, that were abundant, were said to be "responsible for much of the predation", though no actual observation was cited, and four other species of birds "may also have been responsible for some of it". Wrens eat few moths, or items as long as 1cm. (B.W.P. 1988). At a site near Birmingham they had "no direct evidence as to which species were responsible for the predation", that is, predation was not seen. All the information on predation is given in just six lines of text. Some moths stuck to trees are eaten by insects (Whittle *et al.* 1976). At one site, for two days of the six day experiment the trunks became wet as the result of prolonged driving rain and were then very black in colour. Pale typical moths stuck there became very conspicuous and were removed by whatever agent was at work – an example of how, the more obvious they were on the tree trunk (an atypical site) the more readily were they picked off. Had live moths elected to settle there – itself an unusual event – they would presumably have vacated the site when it became wet, and would never have settled there at all had it been wet at the outset.

In experiments on three species of moths including *Biston betularia* and *Diurnea fagella* Steward (1977) gave no information on what removed them from trees, but simply assumed that disappearances were the result of predation by birds, the only mention of which is that more were seen at the experimental sites at one time of the year than another. In all three species, "selective predation of the morphs" was recorded, as was predictable if birds had indeed removed dead moths. Both this paper and that of Lees and Creed are cited by Berry (1990) as among those that confirm "Kettlewell's predation results"!

Steward also made innovative observations on a population of *D. fagella* that frequented a small wood at Cardiff. Having established that over 90% of the males rest by day within 3 m of the ground, he meticulously searched 158 trees up to a height of 2.5 m, counting the moths present. This he did on 20 consecutive days and, using a different colour for each day, marked with a minute coloured dot, 977 males and 22 females, some

melanic, some typical. He counted survivors daily and, although he produced no evidence for this, assumed that the major cause of mortality was predation. That it reflected the inevitable end of the brief adult life was not considered. Particularly curious is that only moths that settled below 2.5 m were counted, yet he was aware that other possible resting sites were available "above 2.5 m on the trees or amongst the leaf litter", as well as on adjacent but un-sampled trees. Some results are enlightening. Of 53 melanic individuals marked on the first day, nine were re-found on day 2, and of this cohort the numbers re-found on days 3 to 10 were 14, 14, 15, 12, 15, 18, 18, and 13 respectively, after which they fell to 5 and dwindled to 1 on days 14 to 16, after which no more were found. No statistical tests are needed to interpret these facts. A greater number present than on a previous day indicates either that some were missed on the previous occasion (unlikely as the search was meticulous), or that the moths dispersed beyond the limited portions of the trees inspected. Steward refers to males beginning to fly vigorously at dusk on warm evenings. The very first sequence is enlightening. That twice as many of the moths marked on day 1 were recorded on days 8 and 9 than on day 2 demonstrates longer survival than day 2 might suggest, and proves that they disperse beyond the confines of the testing ground. Some may do so, never to return. From such counts it is impossible to calculate mortality, let alone attribute it to specific causes. Non-melanics displayed the same behaviour, but as numbers were fewer the results were less striking. The idea for the experiment was excellent: its implementation and interpretation flawed.

The biology of the moth is highly significant. As flightless females were plentiful on the same trees at night, males would have no difficulty in finding mates. One night's activity was probably sufficient for a male to fulfil its destiny. Thereafter it was expendable. Predation levels on males that can be active for up to at least 10 days were clearly of scant significance. Shorter survival is sufficient. If the 53 melanic males recorded on day 1, and their survivors, suffered 10% predation per day, and no other mortality, just over half would still be alive on day 8. Even though dispersal beyond the confines of the sampling site occurred, and some may have died, rather more than a third were re-found alive on that day. As Porritt noted more than a century ago, females, the guardians of the genome, put themselves largely out of reach of predators. The shape, small size, and often the abundance, of males of *D. fagella* combine to offer what appear to be more suitable targets to birds than do large moths and Steward cites others as having recorded them as prey. His experiments, however, give no indication that predation is a serious hazard.

Porritt's eclectic interest in many species enabled him to appreciate that the situation was complex; that the pattern of development of melanism, and the underlying mechanisms, were not the same in all species; that differences in *behaviour* in different species made it impossible to specify a universal explanation of the significance of industrial melanism; and that species which reacted to conditions that apparently induced melanism in a considerable array of moths by becoming paler, made universal pronouncements almost impossible. So too did the example of species such as *Acronicta menyanthidis* that persistently remained pale in a smoky area where melanism was prevalent in many species, yet which was present largely in the melanic form in not far distant areas where there was little smoke. These observations and deductions are seen to be all the more meritorious when it is remembered that all were original, though discussed with fellow naturalists, and were made more than a century ago by an amateur investigator. They were first rate natural history. By way of comparison, in spite of the enormous amount of attention paid to the phenomenon of industrial melanism in the Peppered Moth, there is still no universal agreement as to how some of the findings should be interpreted, and the validity of some of them is suspect. Indeed Majerus (1998) asserted that the story of the Peppered Moth was "wrong, inaccurate and incomplete" in most respects – though he still accepted the influence of "differential bird predation" as an important element in it – and more recently expressed the view that the general picture is much as the long promulgated story claimed! Thus, in rejecting objections to the widely accepted view, Majerus and Stevens (2006) maintained that the story of the Peppered Moth is an excellent

example of Darwinian evolution in action. However, they made no reference to the anomalous spread of melanics into clean areas and their rise to dominance there, yet these events indisputably negate and repudiate the very principles on which the original story was founded. Until these events, which embraced enormous areas of countryside, and were enacted in exactly the same way by other species, some of which are never exposed to any predation by diurnal birds, can be explained without contradicting long-held beliefs, the orthodox story is comprehensively refuted.

Grant (1999) drew attention to the way that textbook accounts of industrial melanism tended to dwell on its spread and (at least at that time) said relatively little about its subsequent decline, though the latter is much better documented. However, he made no reference to the phase that separated these events, when melanics spread beyond the industrial zone and became established over extensive regions, and in so doing pose questions that are difficult to answer, or contradict some of the claims that have been made. He also made the categorical statement – that would doubtless be endorsed by many – that "no other evolutionary force can explain the direction, velocity and the magnitude of the changes except natural selection". These assertions are based on *B. betularia*. However, when one considers the many other species that display the phenomenon, the situation is seen to be vastly more complex than might be deduced from considering this species alone, and his claim is easy to refute. Indeed the categorical assertion about natural selection is open to challenge in *B. betularia* as well as in other species. As Williams (1966) put it, "a biologist can make any evolutionary speculation seem scientifically acceptable merely by adorning his argument with the forms and symbols of natural selection." How, for example, can extension of the range of melanic individuals of this species beyond the limits of soot-blackened areas be explained? These were no minor incursions. Melanic *B. betularia* colonised suitable habitats throughout the whole of Yorkshire and eventually comprised over 95% of the population. Melanic forms of other species behaved likewise. Natural selection did *not* match moth to background here. Emphasis on one species also obscures the fact that natural selection could not possibly have been responsible for the increased incidence of melanism in species that remain hidden by day and are never exposed to this process insofar as coloration is concerned. What is more some of them became melanic much more rapidly than did *B. betularia*, the 'model' species that is all too often considered as representative of events that took place, when only the consideration of each species involved can provide the necessary information. Even Grant's claims for *B. betularia*, can be challenged. Thus his assertion that "none of the implications so far identified have challenged the role assigned to selective predation as the primary explanation for industrial melanism in Peppered Moths" is easily refuted. If, as his argument demands, pale individuals are selected by predators in industrial areas, melanics must be selected in clean areas, yet when the melanic form of this species extended its range into such areas it did so in spite of any such selection against it. A claim that a phenomenon has been demonstrated by one set of observations but is flatly contradicted by another is on quaking ground. Moreover, experiments have indicated that neither typicals nor *carbonaria* show any preference for a matching background, which seems to negate the possession of this aid to survival. The brevity of the life span of the adult moth also conspires to thwart natural selection. Adults are exposed to it for only a very short time.

Not all observations agree with the usually accepted story. Murray *et al.* (1980) cast doubt on the claims of selective predation. They stuck dead moths (*B. betularia* and *Apocheima pilosaria*) to trees and attributed any disappearances to removal by birds. They watched birds at the site, whose absolute numbers are unclear. In 46 hours of watching (summer and winter) they saw one *B. betularia* removed by a Blackbird – a species one does not associate with searching tree trunks. Seven unidentified moths were taken from trees by birds (four species), which does not imply heavy predation. Particularly important, although displayed moths disappeared "there was no significant difference between the rate of loss of different morphs of the same species" and they concluded that "other phenomena need to be invoked to explain the existence of polymorphism for melanism." This was in

keeping with earlier cited work which they interpreted as indicating that "selection other than that exerted by predation is associated with melanism in moths". Even earlier, Bishop and Cook (1975), who had doubts about the validity of using dead moths in experiments, had wondered whether the assumption that natural selection took place as a result of selective predation by birds may be mistaken.

THE SCALLOPED HAZEL, *ODONTOPERA BIDENTATA*: A TEST CASE FOR THE SPREAD OF MELANISM VIA RANDOM MUTATION AND SELECTIVE PREDATION

Among the many species known to Porritt before they became melanic in the late 19th century was *Odontopera bidentata* with which he was familiar for 30 years before, in about 1896, "a quite black specimen" was taken at Wakefield. Thereafter, in Wakefield and Methley, some 5 miles away, the melanic form rapidly became common, and Porritt, who reared such individuals, reported that in 1905 George Parkin of Wakefield estimated that the increasing incidence of melanics was so rapid that "in a few more years the pale form will be quite eliminated". While he was not correct to predict complete elimination, *O. bidentata* became predominantly melanic. This form indeed became abundant and widespread in South West Yorkshire and South Lancashire and, much later, was intensively studied by Bishop *et al.* (1978a, 1978b) in the latter region.

Although its larvae are often abundant, as Moses Harris recorded in his 'Aurelian' (1766) it is "seldom taken in the Fly State". On its secretive habits, Mosley (1883), one of Porritt's co-workers, threw interesting light. He found that by day it frequented out–buildings and also crept into corners of doorways and windows, where – its colour irrelevant – it was certainly free from attack by birds. In assembling traps it moves into corners, thereby confirming Mosely's observations on its behaviour. Its secretive nature is made apparent by the fact that although Bishop *et al.* (1978a, 1978b) revealed it to be very abundant, they confessed that they did not know where it rested by day. They found only one individual in a natural resting place – in a crevice – and suggested that it "may hide under leaves and in crevices in the wild". They say it does not rest on exposed surfaces in S. Lancashire, but in some areas it has been found doing so on walls and fences (Skinner, 1984), and was said by Mays (1986) in his commentary on Harris (1766) to do so in the London area. Apart from those individuals that in some places rest safely in the open by remaining motionless, vast numbers are so well hidden as to be free from predation by birds. No record of it being taken by a bird has been found, nor do Bishop *et al* record such. Bishop *et al.* (1978b) estimated its abundance near Liverpool and cite densities of more than 25,000 / km^2 and c. 400,000 / km^2 per flying season, mostly concentrated into about three weeks. It is vastly more abundant there than *Biston betularia*. That this moth is so abundant, yet in the course of an intensive study of its biology they found only one individual as a result of daytime searching, bears striking testimony to the efficiency of the way that it hides itself. It is *not* exposed to natural selection by birds that might feed on it.

These workers also carried out predation experiments, exposing moths on tree trunks, walls and leaves on 29 days. Of 81 melanic and 81 non-melanic moths exposed, in each case 27 were taken, with no significant difference on any surface. They did likewise in Woodchester Park, Gloucestershire, where the population is entirely non-melanic, exposing 69 individuals of each morph on two different surfaces over a 6 day period. Of these, 26 melanics and 27 non-melanics were taken. More clear cut results can hardly be desired. All demonstrate categorically that even if the moths were exposed to predation in nature – which they are not – neither melanic nor pale forms would be selected. Against the backgrounds used, both morphs may be equally conspicuous to bird vision.

O. bidentata exhibits to perfection a trait common to many nocturnal moths. Its habits ensure that it is essentially immune from predation by diurnal birds, and therefore from any selective effects exerted by such predators. Notwithstanding persistent claims that predation by birds determines the success or otherwise of a particular morph, the melanic form spread into unpolluted countryside. That this is in harmony with the results of experiments which revealed no discrimination by predators against the melanic form is in

fact probably of no consequence in this respect. The spread was achieved by a species that is simply not accessible to birds. No selection, on the basis of melanism or otherwise, was involved, nor can it have been involved in the declining incidence of melanics currently in progress.

The situation in *O. bidentata* is helpful in the quest to understand the significance of industrial melanism in moths, and comparison with *B. betularia* is particularly enlightening. Melanic and non-melanic (typical) forms of moths might reasonably be supposed to have advantages and disadvantages under different circumstances. Melanism has been supposed to be advantageous in soot-blackened conditions by rendering moths less conspicuous to predatory birds than are typicals. Moreover, as Cook (2003) put it in a thorough review of the history of melanism in *B. betularia*, "The strength of selection may be estimated from frequency changes"; i.e. if the frequency of melanics falls over time it is assumed that there is selection against that form, and against non-melanics if it rises. He calculated the disadvantage suffered by the *carbonaria* morph in numerous areas during its recent decline in incidence, a decline generally attributed to selective predation by birds. While the calculations are beyond reproach, it is arguable whether the assumed causes of these changes – namely changes in predation pressure – are indeed responsible. This is easily demonstrated by considering the situation in *O. bidentata* in which there has been a recent decline in the incidence of melanism just as there has in *B. betularia* – a situation that is discussed later. However, this is certainly *not* attributable to changes in the strength of selection exerted via predation by birds, because, by virtue of its habits, *O. bidentata*, like several other species that became melanic and are now changing in the opposite direction, is exempt from such predation. To find a hidden adult is a rare event, and there is no evidence of predation. Until such is *demonstrated* it has to be accepted that there is nothing to show that adults are ever taken by birds. If the decline of melanism in *O. bidentata* has nothing to do with changes in predation pressure, why should this not apply also to *B. betularia*, for which species there are apparently no observations of predation on truly wild moths, and certainly no concrete information on changes in the intensity of any such predation pressure?

An orthodox interpretation of the rapid spread of melanism in *O. bidentata,* witnessed by Porritt and his fellow entomologists would necessitate a substantial mutation rate, accompanied by intense selection in favour of the melanic form. Mutation rates in nature generally range from about 10^{-4} to 10^{-10} per generation, which would be woefully inadequate to meet requirements and, far from there being intense selection that rapidly eliminated individuals of the typical form, there is no evidence whatever of any such selection. The almost universal belief that in industrial areas there was differential selection in favour of the melanic form via predation by birds on non-melanic individuals did not happen. The moths are not exposed to such predation and neither morph suffers any predation from visually hunting predators. The key problem therefore is to explain how random mutations were able to produce melanics that persisted and gave rise to offspring that, in a few years, dominated the population. No such explanation is possible. That most frequently alleged demands a mutation rate far greater than that which appertains in nature, and random mutation without selection is powerless. If melanics were not selected as a result of the elimination of non-melanics by birds, how were they selected? What possible agent can be suggested? Bishop *et al* (1978b), were aware of this discordant situation and, cautiously but correctly, conclude that "Selective predation has yet to be demonstrated as being of widespread significance in determining morph frequencies in populations of *G.* (= *O.*) *bidentata*". One can go further than this and state categorically that in polluted areas natural selection via bird predators which preferentially take the pale form to the benefit of the melanic form did *not* take place. Nor did the converse take place when this species colonised rural countryside from smoke-blackened areas. As Endler (1986) has pointed out, the most important problems in detecting natural selection arise out of incomplete knowledge of the ecology and general biology of the species studied. In this case the biology of the moth is sufficiently well known to enable it to be firmly stated that

no selection of any kind is exerted via predation by birds. A suggested explanation of the spread of melanism without selection in this and other species, for which evidence relating to the moths themselves is supported by findings in very different fields, is given immediately after the next section.

THE DECLINE OF MELANISM IN UNPOLLUTED AREAS

Majerus (2007) studied *B. betularia* near Cambridge between 2001 and 2007, at a time when the melanic form, which had successfully (and incongruously) colonised the area from its industrial strongholds and eventually dominated it, had been in decline there for more than three decades, though there were no clear indications of any ecological change that could have tipped the balance against it. He offered moths to birds in nature, taking care to avoid some of the mistakes made in earlier investigations. Predictably, melanics, the more conspicuous of the two forms against the backgrounds utilised, were taken in disproportionately greater numbers than typicals. The only result that would have been surprising would have been if non-melanics had been taken preferentially. These predictable results in no way resolve the major, but unacknowledged, problem presented by *B. betularia* in the Cambridge area. That problem is why, if, as Majerus claimed, predation by birds is important, and they select the most obvious individuals, had the melanic form been able to colonise and dominate that unpolluted area? Can it be denied that, had he carried out experiments whilst this colonisation was in progress, melanics, the more conspicuous of the two forms, would have been preferentially predated just as they were in his experiments made when it was in decline? This is the key question. In fact they increased their representation in the population against any such predation exerted by birds.

In fact such experiments *were* carried out at two sites in East Anglia at an appropriate time (i.e. 1973) by Lees and Creed (1975). The incidence of the invasive *carbonaria* passed its peak in the area in the 1960s (Kettlewell, 1973) but this form still greatly predominated and, on the basis of small samples, did so at frequencies of 64.1 and 67.6 at the time of the experiments. Frequencies of the typical form were only 21.9 and 17.6 respectively, the 'missing' element being made up by representatives of the *insularia* form. Dead moths from bred stock, kept deep frozen, were displayed on tree trunks. Predictably *carbonaria* was preferentially selected because it was the most conspicuous. So conspicuous were the displayed moths that, although presented in modest numbers, they became essentially feeding sites for birds and had to be visited every two hours and, on day 5, at half–hourly intervals, to record the removal of offerings. So disruptive was this that, on day 6, the experiment was moved to another wood where inspections were made every 3 hours. Other than showing that the conspicuous *carbonaria* was the most frequently taken form on all six days, there appears to be no good reason for believing that the results revealed much about events in nature, where sparsely distributed, better concealed, and short–lived moths that had selected their own resting sites, may not have been eaten at all. What is absolutely clear is that, while such melanic individuals as were detected by birds in nature may have been eaten, their colonisation, spread and rise to dominance in the area, unequivocally demonstrate that any such predation was ineffective. This not only puts the claims of Majerus in perspective but negates a key premise of the classic story of industrial melanism that is based primarily on the history of the species concerned.

One might also ask why, if, as might once have been claimed, melanics enjoy greater fitness than the typical form, is their incidence currently in decline near Cambridge? By the same logic as Majerus applied to the situation in the first decade of the present century, when he claimed that "differential bird predation here is a major factor in the decline in *carbonaria* frequency", [which he did *not* demonstrate] the melanic form should never have established a significant presence there. Melanic individuals should have been preferentially preyed upon by birds. His claim is entirely illogical and unacceptable unless an explanation of the earlier increase of melanics is provided. Remember, the area colonised was clean countryside, not an industrial area. The nature of the background remained essentially unchanged throughout: in industrial areas it changed from 'pale' to

black, then reverted to 'pale'. Moreover, he did *not* demonstrate that differential bird predation was a major factor in the decline of the melanic form that was in progress during the period of his experiment. The incidence of melanics was in decline before the experiment began. He had no means of measuring the contribution made to that decline by bird predation, if any, and, for all the care bestowed on them, the experiments involved un-natural presentation of moths to birds. It seems highly probable that, just as melanics came to dominate the population in spite of the adverse effects of any such predation – which his argument demands – their decline would have taken place whether predation exerted any effect or none. Melanic forms of several species that colonised clean from polluted areas elsewhere, are in decline, e.g. in Yorkshire. These include *Odontopera bidentata*, adults of which are hidden by day and are not subject to predation by birds.

Just as predation *may* have slowed down colonisation of the area by melanics, it *may* be hastening their demise, but it can no more be claimed that it is *controlling* this process than that it controlled the increase in melanism there – which it manifestly did not. It was certainly *unable* to control the incursion and spread of melanism and it is illogical to claim that it is responsible for its decline. Nature conducted the first experiment (colonisation by melanics): it is currently conducting its counterpart on an equally large scale. The trend of the second experiment is also perfectly obvious and, barring unanticipated environmental changes, the result is entirely predictable.

Majerus (2009) reiterated his earlier belief (1998) that in polluted regions the rise and fall of the melanic form of *B. betularia* was the result of differential bird predation, with some migration, "almost to the exclusion of other factors", though he did not demonstrate this. Indeed he did not cite a single instance of a Peppered Moth being taken by a bird in a truly wild situation. He also commented that this was the view of most of those who had considered the matter. This does not make it correct. Porritt, an early sceptic, was one who disagreed, though not with *B. betularia* alone in mind. Abundant evidence demonstrates conclusively that some species which became melanic are completely exempt from predation by birds and that differential predation on a particular morph had nothing to do with the onset and spread of melanism in these species in industrial areas in the 19th and early 20th century, or with its subsequent decline. Evidence for predation on *B. betularia* is based entirely on un-natural situations, and there is little to suggest that it is subject to much predation by birds. Bats, which are oblivious of colour differences, are a different matter, but their sometimes substantial depredations are non-selective.

Recent changes in the incidence of melanics in clean areas from which they had largely ousted the typical form, were sometimes rapid. At Spurn, Yorkshire, since 1998 most *B. betularia* have been typicals. Prior to that year "there was a rapid change over about three years from the majority being melanic to the majority being typical" (B.S. Spence, cited by Beaumont, 2002), a trend that continued to 2010. There was no obvious change in the nature of the background that could explain this change in fortunes of the two morphs. Nor can it be claimed that natural selection was involved when it had clearly failed to prevent the reverse process some years earlier when melanics ousted the typical form. There was no matching of moth to background here. Spence, who has trapped moths at Spurn for 30 years, and currently runs three MV traps, has no recollection of ever seeing *B. betularia* resting by day, other than those just released from traps, and has "certainly never seen a bird take one".

THE COMPLEXITY OF EVENTS IN THE INDUSTRIAL ERA: CAN THEY BE INTERPRETED?

That, beginning in about 1880, more than 40 species of moths became melanic in South West Yorkshire in a period of less than 30 years is remarkable. That mutation rates were sufficiently high to provide the raw material for such rapid transformations seems highly improbable. They would have to be much higher than those that generally prevail. That this happened in so many species strains credulity even further and, in some species, the brevity of the adult stage, during which selection acts, is also relevant. Even more remarkable is

that in several cases it is not only very difficult to believe that melanism was established as a result of natural selection, but demonstrably certain that it was not. As Porritt made clear, almost the entire population of *Colostegia multistrigaria* became melanic within about 10 years, and females of *Apocheima pilosaria* and *Agriopus marginaria*, which did so by a different genetic route from the males (which took somewhat longer) did so in no more than six years, i.e. six generations. That melanism spread at such a rate might be interpreted as indicating that it conferred an enormous selective advantage. However this is untenable. *C. multistrigaria* remains hidden during the daylight hours, as do the females of the two latter species and of *Diurnea fagella* and most of the males of *A. marginaria*, and are therefore never exposed to those selective forces that have been supposed to favour melanism. The same is true of both sexes of *Odontopera bidentata*. Nor need their rapid transformation, nor their persistence as melanics, necessarily imply that they were selected. All that can be inferred from the remarkable change is that it was not sufficiently detrimental to have been selected against. In other species that became melanic this may have been advantageous, or simply non-detrimental. Each has to be considered on its merits. That so many species became melanic so quickly in the same restricted area, is in fact only one element, though the most striking, of a complex situation. Other species behaved in exactly the opposite way: they became paler. This fact, made clear by Porritt and Morley more than a century ago, seems never to have been appreciated. Something affected pigmentation, and not simply in a phenotypic but in a heritable manner. It is, however, difficult to postulate that the increase in melanisation that was involved in many cases was adaptive when some species clearly did not enjoy any obvious benefit from the acquisition of this attribute and others, sharing the same blackened environment, became pale and not dark!

A new element was introduced into the interpretation of industrial melanism when, following earlier work by Harrison in 1920, Harrison and Garrett (1926) and Harrison (1928) claimed to have induced heritable melanism in moths by feeding larvae on plants contaminated by salts of lead and manganese. Criticisms were comprehensively answered by Harrison (1935). The concept of inducement of a character is prone to misrepresentation. Most mutations arise 'by chance' for reasons unknown: molecular changes in DNA occur and are inherited. That a stress, or hazard, that causes a gene to mutate can be identified, and that it can then be deliberately applied, enhances understanding of the evolutionary process. Harrison and Garrett listed crosses made in the Early Thorn, *Selenia dentaria* (then *bilunaria*) and *Ectropis bistortata* and precisely itemised the offspring in the text and in 23 tables. The results were clear and unambiguous. There is nothing unscientific in suggesting that the mutations involved were induced by the environment. Harrison was indeed a pioneer in this field. That his views, of which Harrison (1927) gives a synopsis, had what some deemed (unjustly) to be Lamarckian undertones does not nullify the facts recorded. The mutagenic effects of mustard gas – dichlorodiethyl sulphate – first tested on *Drosophila*, were discovered in 1940-1941 by Auerbach and Robson but, because of wartime restrictions, were not made known until 1946 and subsequently. Many chemical substances are now known to have such properties. They join X-rays, UV radiation, and others as means of inducing mutations experimentally. Moreover, chemical mutagens can produce heritable changes.

Ford (1937, 1964) and Kettlewell (1961, 1973), who made no attempt to refute the results, dismissed these detailed demonstrations as being of no significance because, so they claimed, the melanics induced were all recessive. In fact Harrison and Garrett clearly demonstrated the inheritance of dominant melanism in the Small Engrailed, *Ectropis crepuscularia,* with which species breeding experiments were not taken very far because of rearing problems. As Harrison (1927) made clear, he was fully aware that recessive melanics were unusual – he described the induction of both dominant and recessive examples but could hardly ignore the results obtained. Incidentally, among the many recessive aberrations of *Abraxas grossulariata* the famous *varleyata* is predominantly jet black. [That melanism is dominant in *E. crepuscularia* and recessive in *E. bistortata* is of

taxonomic interest as the distinction between the two species, which is not easy on morphological criteria, has been questioned at times. This biological difference, like overlapping flight times, supports their distinctness.] The objections do not rule out the possibility that some component of the pollutants, generously spread in industrial areas, induced mutations. Ingestion of contaminated food by larvae is an obvious route. That a salt of lead was identified in this role by Harrison and Garrett reminds us that ice cores from Greenland subsequently revealed an increase in lead in the environment at the time of the industrial revolution, but it now seems more probable that some organic compound, present in minute amounts, was the active agent. If mutations that gave rise to melanic individuals were induced by such unnatural means, this would explain the amazingly rapid replacement of typical by melanic forms in some species reported by Porritt (1907) – which had already answered the criticism of Fisher (1933) that the induction experiments demanded a mutation rate greater than that found in natural populations. Melanism could have been induced simultaneously in many individuals by a pervasive chemical, which would ensure its rapid spread, whereas relevant random mutations would be expected to arise infrequently, in few individuals, and the trait to spread more slowly. Indeed the rapidity with which melanism spread in several species – which is inexplicable on the basis of random mutation rates – is a major stumbling block to those who seek to explain industrial melanism as the outcome of such mutation, followed of course by natural selection. Here natural selection is completely exonerated from participation in many, perhaps in all, cases. Curiously one of the reasons given by Ford (1955) for rejecting such induction was that the mutation rate would not be sufficiently great. Another objection (Ford 1955, 1964), that the mutagenic effect of Harrrison's suggested mutagens would have to be thousands of times greater than that of powerful doses of penetrating radiation is nonsense. Time-wise, it appears that if mutagens were indeed responsible, apart from their possible effect on *B. betularia* (which, although affected early, reacted more slowly than most?) they reached a level in S. W. Yorkshire that rendered them effective by about 1880, following which many species were affected.

Fisher (like Ford and Kettlewell) was unaware of Porritt's observations on more than 40 species, which showed that they became melanic at a rate that they deemed to be impossible on the basis of the spread of mutations. Harrison and Garrett were probably fortunate in that the treatment they used incorporated the mutagen. Others, like Hughes (1932), were not. None of this negates what Porritt observed. In his area the mutagen, whatever it was, was probably omnipresent, as it may well have been where Harrison and Garrett carried out their experiments – which would nullify the arguments against them. The identity of the mutagen, of whose effect in Porritt's area there is abundant evidence, is still unknown. Their statistical virtuosity notwithstanding, the arguments of Fisher were rendered irrelevant by the fact that the situation did not reflect the operation of random mutations – which do not occur at such high rates as were clearly involved. The situation can, however, be explained if the causal agent was a mutagen. It should also be noted that Fisher did not condemn Harrison and Garrett, and in fact concluded that the work of Hughes was insufficient to show that "chemical agencies do not induce mutations with even more than the high mutation rate of 1 percent", and that the evidence against the induction of melanic mutations was insufficient to disprove the existence of mutation rates of up to 5% or even 8%. In cases where melanism was acquired more rapidly in females than in males, the mutagen may act at different rates in the two milieux, but speculation is unhelpful.

In brief, abundant evidence demonstrates how the pervasive effects of a mutagen induced the rapid spread of melanism, and did so without the intervention of natural selection, which is the indispensible accompaniment to random mutation in the normal course of evolutionary change. That some species became pale is in harmony with the idea that chemical mutagens which upset pigment metabolism were responsible for the changes in pigmentation. In most cases an excess of melanin was induced: in others paleness can be attributed to impairment of melanin synthesis. The facts are in full conformity with this suggestion. That so many species began to display abnormal pigment synthesis or

metabolism, indicates a very unusual state of affairs. One would not expect similar mutations to arise by chance in so many co-existing species in a restricted area. Moreover, a parallel situation arose in polluted areas in North America that involved a suite of different, but sometimes related, species from those in Britain. That this should happen by pure chance stretches credulity beyond its limits. Relevant also is work by Waddington in the 1950s on what he called genetic assimilation, which gave rise to such dramatic modifications as those that transformed the third thoracic segment of *Drosophila* into a replica of the second, which was inherited, and cautions against dismissing the results of Harrison and Garrett.

Strong support for the mutagenic origin of industrial melanism is provided by the phenomenon of insecticide resistance, which also furnishes similar examples of the rapid spread of an attribute. Pesticides to which resistance is acquired are in effect mutagens introduced into the environment by man. There are physiological and molecular parallels between the spread of insecticide resistance and of industrial melanism and in the mechanism whereby melanism is acquired in birds and mammals. Mutagens often operate in a simple manner. Only one amino acid change is necessary to render a mosquito resistant to DDT. The vast number of individuals involved, and the frequency of generations, explains the even more rapid spread of resistance than that of industrial melanism in moths – itself surprisingly rapid. Drug resistance in pathogenic organisms can be similarly interpreted. Such drugs are mutagens. The malaria parasite, *Plasmodium falciparum*, developed resistance to chloroquine – initially a very successful anti-malarial drug. A more recent drug is pyrimethamine. However, *P. falciparum* can counter this by a single amino acid substitution which renders it a hundred times more resistant. The rapid spread of such resistance is facilitated by the vast number of parasites involved and their prodigious fecundity. As many as a trillion individuals of *Plasmodium* may be present in an infected person. This is almost infinitely greater than the size of any moth population in which melanism spread, but where it nevertheless did so with startling rapidity. The waning of the effect of the mutagen responsible for melanism as its level declined also has a parallel in chloroquine. Five years after its use was discontinued, *P. falciparum* was found to be susceptible to it again.

Black pigments are now well studied in reptiles, birds and mammals, in which black mutants occur in many species. Here a single genetic difference is often responsible. A very small difference in a molecular detail, affecting a single amino acid, in the melanocortin-1 receptor, for example, gives rise to the white and 'blue' forms of the Snow Goose. That differences are so small suggests that their induction in the polluted conditions that prevailed in Porritt's area around 1900, and had done so since early in the previous century, would not be surprising. That they should be the consequence of a chemical mutagen is entirely feasible. Such a cause provides an explanation of events, and also of their rapidity. It also explains the eventual disappearance of these variants when the mutagen gradually disappeared as pollution levels fell and its effects waned. The similarity of the molecular processes involved in the induction of melanism and in resistance to pesticides and drugs is striking and convincingly informative. That industrial melanism arose in so many taxonomically diverse species, and that in some species it was certainly not favoured by natural selection for the simple reason that they were never exposed by day, indicates that it was often not adaptive. Ironically, although the mechanism is well understood in birds and mammals, exactly which gene is associated with industrial melanism remains unknown. It may even be that different genes are involved in different species as some of those that display the phenomenon diverged as much as 100 million years ago.

The biology of the North American geometrid *Nemoria arizonaria* is pertinent here. This species is bivoltine. Larvae of the spring brood feed on oak catkins and are knobbly, yellowish mimics of such catkins: those of the summer brood feed on oak leaves, are more slender, less knobbly, greyish green in colour, and mimic oak twigs. The twig mimics also have larger jaws and jaw muscles needed to eat leathery leaves, and behaviour is appropriate in each morph. Unlike adults, larvae are eaten extensively by birds, so

camouflage is advantageous. Experiments using foods kept frozen between seasons revealed that, regardless of season, *all* larvae fed on catkins developed into the catkin morph, and *all* fed on leaves into the twig morph (Greene, 1989). Larval form (not just colour) is *induced* by the kind of food eaten in the first three days of larval life. This illustrates that the following of different developmental pathways, that are genetically coded and involve even morphological differences, can be induced by what a larva eats during a brief period immediately after it emerges from the egg. Oak leaves are rich in polyphenols, especially tannins, and are fibrous: catkins are low in tannins and fibre, and pollen is rich in proteins. Equally relevant, we now know that the profound differences in size, anatomy, life-span and behaviour in queens and workers of honey bees are *induced* in individuals with the same genetic endowment by purely physical external factors. Likewise, in autumn declining temperatures and food supplies *induce* the production of males in populations of *Daphnia* and related crustaceans previously reproducing by parthenogenesis. These mate with females that produce resting eggs which overwinter and hatch as females that reproduce parthenogenetically in the following spring. By comparison the induction of pigment synthesis is trivial. Nature is almost endlessly versatile. Induced changes, even if not heritable, can be of great survival value and therefore of evolutionary importance.

The failure of those, such as Hughes (1932), who sought in vain to induce melanism in moths – which Harris and Garrett successfully did – by feeding larvae on leaves impregnated with salts of lead and manganese can have several possible explanations. In particular, the exact nature of the agent remains unknown: it may be some substance that, in minute amounts, acts synergistically with a particular salt. It may even be that the substance was not present in the clean environment where Hughes carried out his experiments, but was omnipresent in the industrial area where the original work was done. Speculation is unhelpful. Harrison (1956) was eventually moved to refute some of the statements made by critics such as Ford and Kettlewell. He made clear that he never claimed to have resolved the problems of industrial melanism, and in particular that, in 1928, no Lamarckian effect was claimed. He referred readers to the semi-popular work of Wells, Huxley and Wells, *The Science of Life* (1932) citing the 1934 edition, which recognised that he had demonstrated how chemical substances can induce mutation, and that this must be distinguished very clearly from "the Lamarckian method of inheritance".

It is easier to believe that many species suffered interference with pigment metabolism as a result of the mutagenic effects of a chemical agent than that they should become melanic as a result of natural selection acting on chance mutations, not least when species hidden by day and not exposed to such selective forces became melanic. How, for example, might the acquisition of melanism in *Colostegia multistrigaria* or *Odontopera bidentata* of which most individuals spend the daylight hours hidden from view, be explained by natural selection via differential predation on melanic and non-melanic morphs? There appear to be no reports of these species being eaten by birds, and until this is proven a virtual absence of predation has to be accepted. Hidden moths are largely free from predation – and, particularly important, from *selective* predation. If the induction of melanism by a mutagen is not the explanation we are left with an unsolved problem because, certainly in many cases, a predominance of melanism was *not* the result of the differential selection of orthodox mutants.

Grant (1999) suggested that none of the work on mutagens has proved relevant to Peppered Moths, but this is not so. Falling levels of a mutagen explain a parallel decline of melanic *B. betularia* when pollution levels fell as a result of a reduction in coal burning. Clarke and Sheppard (1966) made the earliest observations near Liverpool. Here *carbonaria* declined from a frequency of 93.3-94.2% in 1959-1961, to 90.0-90.2% in 1964-1965, the most relevant smokeless zone being established in mid-1962. For such distinguished investigators the number of assumptions made was remarkable, and inevitably included "predators are the only source of mortality". The selective disadvantage of *carbonaria* was calculated as "between 26 and 90% with a probable value of 58%"

which is not very precise, and they assumed that this represented a steady change in gene frequency between 1959 (why not 1962 or 63?) and 1965 so that the typical form "has been at an advantage of 23%". However, experiments indicated that it was at a *disadvantage* of about 20%, so they proceeded to make more assumptions in order to find "some compensating selective disadvantage" to *carbonaria*. What was overlooked is that alleged selection in *B. betularia* depends on matching the background and *not* on levels of pollution *per se*, and that falls in the latter are not paralleled immediately by cleaner trees and walls. These lag considerably. Soot-blackened stonework persists for many years after the return of clean air. A memorable example, still completely black at the millennium, in Adel, Yorkshire was cited by Fryer and Lucas (2001) and others still abound elsewhere. According to the orthodox story, melanic forms should have persisted in soot-blackened areas long after smoke levels fell. Instead they declined as levels of the mutagen decreased. And of course melanic forms long flourished in unpolluted countryside, which is hardly compatible with the suggested correlation. As the only suggested source of mortality – predation – has no support from observations in the wild, the explanation of events is weak. A decline in melanics to match a fall in the level of a mutagen is more convincing, and has a parallel in the loss of resistance by *Plasmodium falciparum* to chloroquine when this anti-malarial drug was withdrawn for five years. In fact *carbonaria* initially declined slowly near Liverpool: its incidence was higher in 1969 and 1971 than in 1963, but from 1978 it plummeted to about 30% by 1989. (Clarke *et al.* 1985, 1990).

The decline of melanics in clean areas as smoke levels fell in the melanic heartlands can hardly be attributed to reduced matching of the background and a consequent increase in predation. The predation hypothesis is a non-starter here. According to that idea there should never have been melanics here. There was presumably always a steady loss of melanics in such areas as mutagens would be at such low levels as to have little or no effect – which emphasises the failure of predation to eliminate the *carbonaria* form. Melanics would be boosted by continuous colonisation by adults and, in the case of *B. betularia*, by wind-blown small larvae sailing on silken threads, as is known to take place. When the source of such colonists was gradually cut off as levels of the mutagen fell in polluted areas, so too would melanics decline in clean areas. Recent events in the clean Cambridge area are explained if *B. betularia* in which melanism had been induced by a mutagen in industrial areas, successfully colonised in spite of any selective predation acting against it. One suspects that predation by birds, if any, was far less during this process than in even the best experiments – *B betularia* is short-lived, often well dispersed, and selects concealed resting places. Certainly melanics became well established in the area, which is embarrassing to those who hold that selective predation by birds is important, and is entirely contrary to the orthodox story of industrial melanism. As the effect of the mutagen eventually began to wane, just as it did in the source areas when environmental contamination diminished, fewer and fewer mutants arose and the melanic component of the population, also deprived of melanic migrants, inevitably declined. As in the colonisation of the area, predation by birds had little or no influence on this process. This explains the entire sequence of events – colonisation by melanics (which was entirely contrary to what those who claimed that melanics were selected by birds as a result of differential predation on non-melanics in industrial regions would have predicted); their rise to dominance (which was also contrary to expectations and made nonsense of the story of how and why they came to dominate populations in industrial areas); and retreat (which demands that birds, which had failed to prevent the rise to dominance of melanics in a clean area, inexplicably began to prey on them in a way hitherto never done). The role of birds appears to have been inconsequential throughout.

A particularly informative correlation that accords perfectly with the belief that industrial melanism arose as a result of induction by a mutagen, and not via natural selection, is provided by work on *O. bidentata* in South Lancashire. Bishop *et al.* (1978b) showed that this species is "very much less mobile" than *B. betularia*, a feature of its biology beautifully demonstrated in a contour map of the frequency of the melanic morph

(Bishop *et al.*, 1978a) which is greatest in populous industrial areas. This is *not*, as might have been supposed had the true facts not been known, a consequence of natural selection via bird predators, which does not take place. It is, however, in complete agreement with the induction of melanism by a mutagen, the concentration of which is greatest in industrial areas. The low mobility of *O. bidentata* is reflected in the diminished incidence of such melanism in areas of lower concentration.

Porritt (1926), ever alert, accepted the findings of Harrison and Garrett – which he regarded as an advance on the idea of differential predation, "to which I could never subscribe" – but wondered why *Selenia dentaria* should have responded to the inducement regime, when it appeared generally not to be so affected in nature, though he knew of one case in Cheshire. Naturally occurring melanics – ab. *harrisoni* – were subsequently found in Yorkshire. The comment by Morley (1906), who encountered species that were becoming lighter in colour and others that displayed such "bright colours", that "one need hardly be surprised at any strange variation that may develop" is fully in keeping with disturbed pigment metabolism.

As Cook *et al.* (2004) note, the idea that melanism was induced has been "kept alive" by some. Sargent *et al.* (1998) refer to 19th century work on the induction of melanism by low temperatures that is largely of historic interest. More relevant, they are more inclined to give credence to the work of Harrison and Garrett than were Ford and Kettlewell, and are critical of its critics. As well as mentioning Waddington's work on genetic assimilation, and their own observations, they cite work on the inheritance of induced changes in the flax plant. They do not, however, refer to the powerful evidence of induction provided by insecticide resistance or to drug resistance in pathogenic organisms.

The belief that melanism was selected to match moths to the background certainly did not apply to species that spend the day in concealment, of which Porritt provided several examples, and of which others include *Odontopera bidentata*. Indeed many species of nocturnal moths spend the day in situations where they are seldom exposed to light, or to potential predators. Nor did the spread of melanic forms, including *B. betularia*, *O. bidentata*, and others from soot-contaminated areas into clean regions fit the matching scenario. That a match between moth and background was even necessary is thrown into doubt by the range expansion of the melanic form of several species, and by species such as *Lampropteryx suffumata* that became paler as the background became darker, or, like *Acronicta menyanthidis* long remained pale in soot-blackened areas but occurred mainly in the melanic form in a clean area such as Skipwith, and spent the day sitting in full view, or, like *Antitype chi* in which, although it produced melanic individuals, also had a very pale form that rested openly on soot-blackened walls. While it may be argued that survival of the seemingly 'maladapted' *L. suffumata* and *A. chi* reflected a decline in the number of predators in a damaged environment, this argument cannot be applied to the melanic *A. menyanthidis* in the near pristine environment at Skipwith. All in fact suggest that predation on resting moths by birds is not a serious hazard.

There appears to have been a diversity of reactions to the effects of atmospheric pollution and the contamination of vegetation, and some moths give no indication of reacting in any way. Taking all the evidence into account there is little to indicate that such changes as were recorded were related to granting protection from predation from birds: indeed some appear to have rendered moths more conspicuous. This does not rule out the possibility that some species benefited by becoming melanic, but this is generally unproven. One suspects that industrial pollution changed conditions so rapidly and so drastically that, notwithstanding the dramatic increase in the incidence of melanism – probably induced by pollutants and certainly not selected – some species had no time to adapt. Some species of Lepidoptera, both butterflies and moths, in Porritt's area became extinct. In others mutations were apparently induced by a mutagen derived from the burning of coal. These were sometimes of no obvious advantage, or seemingly even disadvantageous, but were tolerated, perhaps being helped by a reduction of competition as a result of some species becoming extinct.

THE HISTORY OF INDUSTRIAL MELANISM: A SYNOPSIS OF SUGGESTED EVENTS

Like nocturnal animals in general, most nocturnal moths are seldom seen by day. When MV lamps came into use they revealed that some hitherto infrequently encountered species were far from rare. Some are completely hidden by day and, with possible rare exceptions, are undoubtedly free from predation by birds. To enjoy such freedom it is not even necessary to be hidden: it is sometimes sufficient simply to remain still. Even easily seen moths, resting fully exposed, are often ignored by birds, as Porritt knew long ago. This can be so even in situations where moths are plentiful. Harrison (1956) recalled how he had recorded in 1920 that moths resting openly on walls near his home in North Durham did so with impunity. For many years he took note of both the typical and melanic forms of *Antitype chi* – the pale form of which so impressed Porritt by sitting exposed and conspicuous on soot-blackened walls. These he counted early in the day and in the evening. Although they were sometimes present in hundreds, he regarded it as an extraordinary event if a single individual of either form disappeared during the daylight hours. Ford, unaware of Porritt's remarkable observations, dismissed those of Harrison as being of no significance by claiming that the two forms are almost equally inconspicuous on the same background. In turn, Harrison was sceptical of what he regarded as the undue emphasis placed on birds as agents of selective elimination. Hooper's book, *Of Moths and Men* (2002) – otherwise not cited because of its alleged bias, though it contains much of interest – records that Sargent told her that around his house in North America moths sat conspicuously in view all day, ignored by insect-eating birds which included Blue Jays, Nuthatches and Woodpeckers. Birds can, however, be attracted to, and induced to eat, moths when the latter are rendered conspicuous under unnatural conditions or presented in excessive numbers. Sargent himself directed a film showing Blue Jays picking up moths – cryptic and non-cryptic – as a demonstration of this. Such feeding is opportunistic. It is not typical.

Early field experiments using *B. betularia* as potential prey for birds were clearly unrealistic, and the same is true to a lesser degree of some of the more recent work. Moths were displayed on tree trunks, which are not the most frequent resting sites, and presented in numbers grossly in excess of those that prevail in nature. To re-emphasise a key fact, all recent experiments are questionable, or invalid, for a simple reason, that seems never to have been considered. It is entirely predictable that moths arranged on a background which renders them conspicuous will be taken more frequently than those that are less easy to see. The more conspicuous they are, the more probable it becomes that they will be taken. The only result that would be surprising would be if the less conspicuous individuals were preferentially selected. One need not be surprised by this failure to recognise what was obvious: like Newton before him, who ignored the consequences of a stationary universe – gravity would cause it to collapse on itself – even Einstein was so wedded to the concept that he (unnecessarily) modified his general theory of relativity to rectify an in-built tendency for space-time to expand.

The cause of industrial melanism has been much debated. What is now certain in several, and probably in many, cases is that it did *not* arise as the result of chance mutations that were subject to, and favoured by, natural selection. It would be surprising if so many species not only produced melanic mutants in the same area in a short period of time, but that these mutants should often come to dominate the populations of these species remarkably quickly as a result of natural selection. Although the rate at which melanics of *B. betularia* replaced the typical form in industrial areas was surprisingly rapid, we know from Porritt's account that many other species became melanic even more rapidly – often several times as fast as did *B. betularia*. Such rapid change alone engenders serious doubts as to whether natural selection was responsible. It is, indeed often undeniable that no such selection was involved, the most obvious cases being those where the moths concerned are completely concealed by day and are never exposed to such selection. A further anomaly is that some species, that co-existed with species that became melanic, changed in the opposite direction and became paler – a problem of which investigators have either been

unaware or have ignored. That *B. betularia* does not select a matching background when it settles casts further doubt on the role of predation by diurnal birds.

The crucial experiments relating to birds and natural selection were made by nature when melanic *B. betularia* and other species that, having dominated the population in soot-blackened regions, colonised large areas of clean countryside and there became more frequent than, and in Yorkshire virtually replaced, typical forms. If selective predation by birds in fact operated, the melanic form would never have colonised such areas. In fact it overwhelmingly ousted the typical. It was able to colonise pristine countryside because selective bird predation either did *not* discriminate against it or, if such discrimination occurred it was indisputably ineffective. The evidence indicates that the intensity of predation, if any, was low. That this ousting was not a consequence of the supposed superior viability of melanics over non-melanics was shown when, still later, with no significant change in the environment to act as a trigger, the typical form began to replace the melanic, which it also did in formerly polluted areas as they became cleaner. This last step, while theoretically explicable as a consequence of natural selection, which would, however, be difficult to invoke as it clearly did not operate when the melanic form was extending its range at the expense of the non-melanic, does not demand such an explanation. The disappearance of melanics is no more dependent on them being removed by selection than was their increase in numbers at the beginning of the story – and is explicable on other grounds.

A single cause can explain all the changes involved in the melanic saga. It explains the origin, and, highly significant, the persistence, of melanic forms in species never exposed to natural selection, in which melanism serves no obvious purpose, and also the otherwise apparently inexplicable cases of species that became paler while co-existing species became melanic. It also explains why the melanic form – supposedly adapted to soot-blackened industrial areas – that had, seemingly inexplicably, colonised the clean areas by ousting the typical form, subsequently yielded up not only this conquered territory but also its former melanic heartland as it became cleaner. All these facts are explained if, during the time of serious environmental contamination, a chemical mutagen, probably ingested by the larvae, disturbed pigment metabolism in *many* species. This often rendered them melanic far more rapidly than would be expected, or would indeed be possible as the result of orthodox mutation followed by natural selection; did so in species that were clearly never exposed to such selection; and caused some species to become paler rather than darker. Its effects clearly persisted during the phase in which melanics colonised clean areas, and only began to wane sometime after conditions became cleaner and levels of the mutagen everywhere declined. The recent decline of melanic individuals in clean areas near Cambridge studied by Majerus (2007) would have taken place without the claimed aid from birds – which, if it occurred at all, must have been going on even when it was changing in the opposite direction and the incidence of the melanic form was *increasing*.

The facts recorded by Porritt – unknown to many subsequent investigators – which at first appear to be anomalous and incompatible with others, and to complicate the usual conception of events, in fact fall neatly into place – as they should because this is what actually happened. Natural selection clearly played no part in the spread of melanism in many species during the industrial era. That predation by birds had little to do with events at that time is also demonstrated by the rapid increase in incidence in soot-blackened areas of *pale* forms of several species, some of which sit openly on display and must be very conspicuous to birds. Although the story is in some ways more complicated than generally believed (but in others more simple) it is possible to present a coherent account that, while in several respects very different from what is generally believed, makes sense – as it should because it is in accord with the natural history of the many species concerned and how they actually behave.

It was generally assumed that the acquisition of near complete melanism in *Biston betularia* in about 50 years reflected a pattern of mutation and natural selection. However, although almost universally ignored, Porritt's contemporary account of how melanism

developed in many species of moths during a period of increasing smoke pollution makes it absolutely clear that in several cases, and perhaps in most, or even all, this was *not* the case. Not only was melanism often acquired at a rate that greatly exceeded that seen in *B. betularia*, (itself extremely rapid) – possibly up to as much as ten times as fast in some cases – but in some, and perhaps in all, natural selection was certainly not involved. Some of the moths concerned were never exposed to natural selection via differential preferences of birds taking melanic and non-melanic forms as prey, for the simple reason that they were hidden from, and inaccessible to, birds by day, and never eaten by them. Startling as this might seem, the almost universally accepted explanation of the evolution of industrial melanism certainly did *not* apply, and much of the edifice that purports to represent the story of the phenomenon is therefore clearly untenable. As a much vaunted demonstration of evolution in action, recently championed again by Majerus and Stevens (2006), and Majerus (2009), it is simply wrong. This in no way implies that the concept of evolution is wrong. All that is criticised is the interpretation of some of the facts relating to industrial melanism and the natural history of the moths involved.

The rapid increase in the incidence of melanism in species such as *Colostegia multistrigaria*, and *Odontopera bidentata* in which there is no evidence whatever of selection that favours melanic individuals, is instructive. Mutation alone, even at a rate which greatly exceeds that which might be expected, even in extreme circumstances, cannot explain the rapid transformation that led to virtually universal representation by melanics in *C. multistrigaria* in not much more than 10 years. Other species became melanic even more rapidly, again with no known selective force to direct the trend. Almost all females of *Apocheima pilosaria* and *Agriopus marginaria* that are not exposed to predation by day were shown by Porritt to have become melanic in no more than 6 years. (Males, that did so via a different genetic route, took longer but did so about twice as fast as did *B. betularia*.) There is nothing to indicate that melanism confers any selective advantage on these nocturnal species that are not exposed by day. If it did they would presumably have become melanic long ago, and no species that recently became melanic would be currently losing this trait. In this respect their coloration appears to be irrelevant. It is displayed neither by day nor by night.

It would be curious if many species in a restricted area had mutated by random processes in a similar way in a short period of time (Porritt listed more than 40 that did so in one area in about 25 years), that the same should happen independently in other areas, and, even more curious, that, in the absence of any positively identified selective agent, the phenotypes produced should persist and become almost universal. Porritt was adamant that selective predation by birds was not such an agent, and the retiring daytime habits of many of the moths concerned, that puts them completely out of reach of birds, is self-evident confirmation of this, as are the habits of those few species of which some individuals at least spend the daylight hours sitting openly in view, evidently unmolested by birds. There is, however, a ready explanation of the widespread acquisition of melanism in the area, which also explains the origin of the contrary and curious development of pale coloration in a few species that co-exist with them. A mutagen originating in the products of combustion of coal which affected pigment metabolism in all the moths involved, irrespective of their habits or genetic relationships, appears to be responsible for all. Highly significant is that the production and effect of such a man-made mutagen have counterparts in insecticides to which resistance has developed in wild populations, and in drugs to which resistance has arisen in pathogenic organisms. Moreover, the genetic effects, that involve small changes in a single amino acid, as they do in the control of melanism in birds and mammals, share striking similarities in all. Both the insecticides and the drugs are, in effect, man-made mutagens. That the incidence of melanism subsequently began to fall as levels of pollution fell is in perfect accord with expectations. There was no change in the level of predation as the incidence of melanism began to fall: it remained essentially nil. The subsequent history of *B. betularia* strongly suggests (indeed virtually confirms) that it too owes its melanic phase to a mutagen.

THE SUPPOSED ROLE OF PREDATION IN THE EVOLUTION OF INDUSTRIAL MELANISM

Even in Britain there are many hundreds of species of nocturnal moths, some common or abundant, yet of which very few individuals are to be seen by day. There is nothing to indicate that they are of much interest to birds as food, and much that shows they are not. Being seldom seen they do not easily present a search image. They are out of sight and out of mind. Many species take refuge among vegetation and plant debris, and when disturbed promptly seek to return to such cover. Some are completely hidden throughout the day. These include species that became melanic during the industrial era, yet clearly melanism is of no significance in such species as a means of conferring protection against predation by birds. They are free from such whether they are melanic or not, and comprehensibly contradict the belief that melanism in industrial areas was established as a result of the selective removal by birds of non-melanic individuals and the consequent survival of an ever greater proportion of melanics in the population. No such selection took place. The rapidity with which melanic individuals came to dominate the populations of several species also demonstrates that to attribute the changes to natural selection was unrealistic. This is unambiguously so in cases in which complete or near complete absence of selection by birds can be demonstrated. It also rules out the possibility that industrial melanics of some of the species concerned were derived from polymorphisms in rural areas that became more common as conditions required (Cook, 2003). The demanded process was too rapid to have been achieved by natural selection. In no case can selection be convincingly demonstrated. Even species that remain exposed seem often not to be of much interest to birds as potential food. Some sit fully exposed throughout the day, as did pale individuals of *Antitype chi* that Porritt long ago recorded in plenty on smoke-blackened walls, and melanic individuals of *Acronicta menyanthidis* that displayed themselves on pale backgrounds.

For *Biston betularia*, which sometimes uses more superficial hiding places, there is no convincing evidence of predation by birds in nature, and it is impossible to know when hiding places have been overlooked. The brevity of its adult life span means that potential exposure to birds is never long, and the taking of a truly wild individual by a bird may even be unrecorded. Harrison (1956) reported some personal observations on this species that caution against the uncritical acceptance of generalisations. Thus, contrary to what is generally suggested, in a very heavily industrialised area of North Durham, although trees of various species were devoid of lichens, they were light in colour, and individuals of the *carbonaria* form placed there were clearly visible at a distance of more than 20 yards. He also reported that on various trees "it is perfectly easy to discern specimens of typical *and* black forms...at very considerable distances" and, particularly pertinent, that when he placed typicals and *carbonaria* on lichen-covered bark, in every trial made, as confirmed by many observers, "the typical form was, by far, the most conspicuous". Such observations hardly support the text book story. That birds do not to a significant extent differentially select melanic or non-melanic individuals according to whether they match their backgrounds by taking those that do not, was conclusively demonstrated when the melanic form of the *B. betularia* extended its range beyond the confines of soot-blackened areas in which it had originated, and colonised unpolluted countryside. If selective predation by birds had led to the establishment of the melanic form in industrial areas, it should have been equally effective in preventing the colonisation of uncontaminated areas by selectively removing melanic individuals that appeared there: but it did not. The melanic form came to dominate the population over large areas just as it had in industrial regions. One such region is the Cambridge area. Nevertheless, Majerus (2007) claimed that predation by birds is responsible for the current decline of the melanic form now in progress there. How, first, this form ousted the typical, then, with no obvious change in the environment, the situation completely reversed, is not explained. If birds are currently eliminating the melanic form by preferentially selecting it, why did they not prevent it from becoming common in the recent past? It has always been the more conspicuous form there.

Majerus is in effect claiming that birds are doing to *B. betularia* exactly what they conspicuously failed to do when the melanic form invaded the area. When, why, and how, did they change? The illogicality of the claim, and the failure to explain the increase in incidence of the melanic form in the area in the recent past, do nothing to suggest that the relationship between birds and adult Peppered Moths is understood. One suspects that they rarely interact.

Natural selection was not responsible for establishing melanic moths in industrial areas for the simple reason that, as is indisputable in certain cases and almost certainly true in most, birds never come into contact with moths that are hiding by day. (Occasional stray encounters are irrelevant.) Nor, for the same reason, was selection able to prevent the colonisation of clean areas by melanic moths from industrial areas. In species that are perhaps less well concealed – such as *B. betularia* – if natural selection had been effective it would have removed conspicuous melanic individuals as they attempted to establish themselves outside industrial areas, but it did not. As Porritt recorded more than a century ago when, for example, he pointed out that *Colostegia multistrigaria* is "absolutely out of evidence until dusk", being hidden in thick grasses and other vegetation by day, and that females of *Apocheima pilosaria, Agriopus marginaria* and *Diurnea fagella* do not frequent tree trunks by day though they may be abundant there after dark, many species that became melanic are not readily available to diurnal birds. Flightless females of *D. fagella* can run rapidly, and can also glide to the ground, snippets of natural history that explain how they can so easily vacate, and return to, their nocturnal haunts. *Odontopera bidentata* is also hidden by day, save for a few individuals that sit exposed but ignored in some areas. Although it is often abundant, even devoted investigators may be unable to find it and, not surprisingly, reports of it being eaten by birds seem not to exist. Experiments using artificially exposed individuals provide little evidence of selection by birds – which would never encounter them in nature.

Insectivorous birds that search terrestrial habitats are not the only ones that pay scant attention to moths. As Porritt (1907) graphically described, "You may go on to one of our heaths on a fine late afternoon or early evening, and see the place absolutely alive with Micro-lepidoptera on the wing, and at the same time the Swallows feeding on the Diptera high up; but they are not taking the moths which are flying in myriads a few inches above the heather". Analyses of the food of the Swallow, and its relatives the House Martin and Sand Martin (BWP 1988) confirm this statement and reveal that Lepidoptera barely feature in the diets of any of these hirundines, which take an enormous range of insects. Porritt, a field naturalist of great experience, was not being naive but emphasising a simple yet important fact when he remarked that the role of Lepidoptera in providing food for birds is largely via their larvae.

Not only was melanism often clearly not acquired as a means of conferring protection against predation, it was also acquired at rates greatly in excess of those that can be explained by natural selection operating on random mutations. Porritt provided many dramatic examples of which he and his contemporaries were witnesses, but of which recent investigators have been unaware. It also arose at what in evolutionary terms was essentially simultaneously in many species of diverse affinities that co-existed in the same restricted area. This, and concomitant cases of species that exhibited a reduction in the production of melanin – for example *Lampropteryx suffumata* gradually became lighter in colour – and therefore became more conspicuous in their soot-blackened environment, points not to differential selection, but to some over-riding mechanism affecting pigment metabolism. This was provided by a mutagen whose appearance coincided with an increase in airborne contaminants in the industrial era, and whose subsequent decline was paralleled by a decline in the incidence of melanism. Such mutagens display striking parallels with pesticides to which organisms have become resistant, and to drugs to which parasites of man have done likewise. Well over 40 species of moths, often active for only a few weeks per year, were affected in about 25 years in the area studied by Porritt. Melanism was acquired with amazing rapidity: almost all females of some species became melanic in less

than seven years. That at the same time as many species were becoming melanic during the industrial era others gradually became lighter in colour, and therefore more conspicuous in soot-blackened areas, can hardly be reconciled with the idea that melanism was selected to protect moths from predation by birds, but is explicable if caused by a mutagen that interfered with pigment metabolism. An explanation based on mutagens also accords well with the clinal nature of melanic distribution that sometimes prevails as one moves from polluted to cleaner areas. A well known cline of the incidence of *B. betularia* between the Liverpool area and North Wales, studied by Bishop (1972) and portrayed diagrammatically in two ways by Bishop *et al.* (1978a), who also illustrate the situation in *Odontopera bidentata* in South Lancashire and adjacent areas, provide detailed examples. Gradients can be equated with changes in the level of mutagens.

As Cook (2003) rightly says of the generally accepted story of *B. betularia*, "the textbook description was simplistic". It was also misleading. Facts presented by Porritt long ago flatly contradict some long held beliefs and assumptions but, although demonstrably correct, have been forgotten. That melanism confers protection against supposed predation by birds in soot-blackened areas was an early assumption, and that its establishment and spread were effected as a result of natural selection via differential predation has been almost universally accepted, yet the facts reported by Porritt make it clear that neither of these assumptions is correct. Subsequent observations have confirmed and extended the evidence that he provided. Ironically the opportunity to test the most promising explanation - the inducement of melanism in industrial areas by a chemical mutagen – by identifying that mutagen, is rapidly vanishing. The ecological changes that provided the background to the drama have been ameliorated and the situation is rapidly returning to that which prevailed before the industrial revolution precipitated the events of the past century and a half.

SOME GENERAL CONCLUSIONS

Industrial melanism in moths, which affected many co-existing species in the late 19th century, arose, *not* as an adaptation, but as a fortuitous consequence of the effect of a chemical mutagen derived from the combustion products of coal that interfered with pigment metabolism. In many cases the result was melanism: less well known, and never explained, is that in others *reduction* of pigmentation ensued, and they became paler – which is difficult to reconcile with the widespread belief that melanism served to camouflage moths against predation by birds in soot-begrimed environments, and that it was selected for this attribute. Mutagens have a perfectly respectable pedigree and are employed to induce mutations in *Drosophila* and other experimental organisms. There are striking parallels between the induction of melanism in moths and the acquisition of resistance to pesticides by insects, and of drug resistance by pathogenic organisms. The responsible agents in all cases are mutagens introduced into the environment by man. The similarity of the molecular mechanism of pesticide and drug resistance and that whereby melanism is achieved in birds and mammals, which involves only a single amino acid, is striking and convincing.

While possibly advantageous to some species, industrial melanism did *not* arise as a result of spontaneous random mutations, which do not occur at rates that are sufficiently high to explain the rapidity with which melanism spread. Porritt, an observer of events in industrial Yorkshire from the 1860s, witnessed dramatic changes in many species of moths in the quarter century that began about 1880. His findings, unknown to most students of industrial melanism, showed that mutations arose and spread at rates much greater than those that do so under natural conditions. Had Fisher, who expressed reservations about the induction of mutations about 80 years ago, known of Porritt's observations his attitude to the situation would have been very different. The spread of melanism in *Biston betularia*, while rapid in its area of origin, was in fact considerably slower than it was in many species that subsequently became melanic in the same area. Populations of some moths became almost universally melanic in about 10 years, and even less in the females of some

species. That this process affected, in what in evolutionary terms was a virtually synchronous manner, many co-existing species, of diverse affinities and habits, that flew at different times of the year, in a restricted area, implies the action of some common cause rather than an oft-repeated independent origin of similar mutations that arose at what were inexplicably rapid rates.

Furthermore, even in the unlikely event that similar spontaneous mutations arose at unrealistically high rates in many co-existing species, this would have served no purpose. As a consequence of their habits, melanic individuals of various species are often not even exposed to natural selection on the basis of this attribute or its alternative. They are hidden by day and therefore almost never exposed to predation by birds – that have been widely claimed to be the selective agents, though concrete evidence of such predation has not been demonstrated in the wild. The spread of melanism had nothing to do with natural selection. Colonisation of clean countryside by the black *carbonaria* morph of the less secretive *B. betularia* – where it sometimes achieved an incidence of >95% after spreading from industrial areas – convincingly refuted the belief that melanism was an adaptation to soot-blackened conditions, and equally effectively negated the argument that birds selectively removed morphs that failed to match the background. Several other species behaved likewise. Other moths that sit conspicuously exposed are ignored by birds if they remain motionless. The effect of birds as predators was inconsequential.

A decline in the incidence of melanics in industrial areas as the environment became cleaner did not reflect natural selection – which in many species was certainly not involved. It reflected the disappearance of the mutagen, whose effects waned also among melanic populations of *B. betularia* and several other species that, contrary to the belief that melanism served to camouflage moths in soot-blackened environments, had established themselves in clean areas. As the effects of the mutagen gradually waned, these areas were deprived of melanic migrants that had earlier topped up the level of such individuals. A similar waning of induced resistance to the anti-malarial drug chloroquine took place after use of that drug was discontinued.

Partly because of inherent difficulties, experiments on predation bear little relation to the situation in nature and the results are always entirely predictable. When moths are offered, the most conspicuous form will *always* be taken in the greater numbers. Such experiments do *not* prove that birds regularly eat these moths in nature. Birds will eat peanuts offered in dispensers, and many other foods that they never encounter in the wild. They will even eat aposematically coloured moths if these are presented en masse. There is no proof that, in soot-blackened industrial areas, birds selectively take (or took) non-melanic individuals of species that became melanic or, often, that they even eat these moths at all. In moths that hide by day it is of no significance whatever whether they are jet black or very pale: their habits ensure that they are never encountered by birds.

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When investigating early Huddersfield naturalists, Alan Brooke unearthed Porritt's York lecture and made notes on it, which I saw in 2007. I hope he feels that this paper goes some way to rectifying the neglect he recognised at that time.

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LICHEN FLORA OF THE WEST YORKSHIRE CONURBATION: A CONSPECTUS

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The West Yorkshire conurbation (WYC) lichen flora has been investigated in detail over the past 43 years by the author and colleagues. It is one of the best documented urban floras in Britain, much of the substantial body of information amassed having been published, including regular updates in *The Naturalist* (Seaward 1978, 1981; Seaward & Henderson 1984, 1991; Seaward *et al.* 1994, 2005 – see also bibliographies contained therein). A conspectus is now necessary, since over almost half a century there has not only been a continuous high level of lichenological activity in the field and in herbaria, but there have also been significant changes in lichen nomenclature and a better understanding of the status of many species.

However, much remains to be done: not only have taxa, such as certain *Lecanora* spp., been overlooked or taxonomically misinterpreted in the past, but the urban landscape and the ambient environment are in a constant state of flux, the ecological and distributional interpretation of the resultant lichen assemblages becoming much more complex in consequence. Air pollution, particularly suphur dioxide, which for more than a century and a half dictated the lichen flora, is no longer the over-riding factor. Therefore, the complexity of the urban environment in terms of the availability of a wide range of substrata subjected to numerous local physico-chemical conditions is now conducive to lichen establishment (Seaward 1997; Seaward & Giavarini 2007); on the other hand, nitrogen products resulting from the extensive use of agrochemicals and the increase in animal husbandry (= hypertrophication) have had a profound effect on the lichen assemblages, particularly those to be found in suburbia and on the margins of urban ecosystems – the luxuriance of these, often dominated by just a few taxa, is evident (Seaward & Coppins 2004). In fact, the local lichen flora within the highly urbanized areas of the West Yorkshire conurbation is often more interesting and biodiverse than that to be found in the surrounding semi-rural to rural landscape due to agricultural practices and the loss of hedgerows, trees and stone walls. Overall, the re-establishment of a diverse lichen flora within the conurbation has been mainly from the north and north-west, the influx of colonists from the east being essentially nitrophilous; lichen re-establishment from other compass directions, as measured by biodiversity, has been less effective. It should also be noted that over the study period, 1967-2010, the urban units (**A–S**) delimited at the start of the investigation (Figure 1) have, due to urban expansion, encroached into the essentially rural areas (**T–W**).

The checklist below identifies those taxa extant within and without the highly urbanized areas of the West Yorkshire conurbation or which have disappeared from them, many being presumed extinct. The following species, previously published as occurring in Yorkshire, are based on doubtful or dubious records (see also list of excluded records in Seaward 1994): *Cladonia deformis* (L.) Hoffm. – uncertain, possibly *C. digitata*, or indeed *C. sulphurina*; *C. degenerans* (Flörke) Spreng. – uncertain, possibly *C. ramulosa* or *C. squamosa*; *Collema nigrescens* (Huds.) DC. – doubtful in the absence of supporting herbarium material; *Degelia plumbea* (Lightf.) P.M.Jørg. & P.James (syn. *Parmeliella plumbea*) – 18th century record from Bradford perpetuated in print from Hudson (1778) onwards is actually from Bradford-on-Avon; *Physcia leptalea* (Ach.) DC. – doubtful in the absence of supporting herbarium material; *Pycnothelia papillaria* Dufour (syn. *Cladonia papillaria*) – doubtful in the absence of supporting herbarium material; *Ramalina polymorpha* (Ach.) Ach. – not this species; *Usnea ceratina* Ach. – doubtful in the absence of supporting herbarium material.

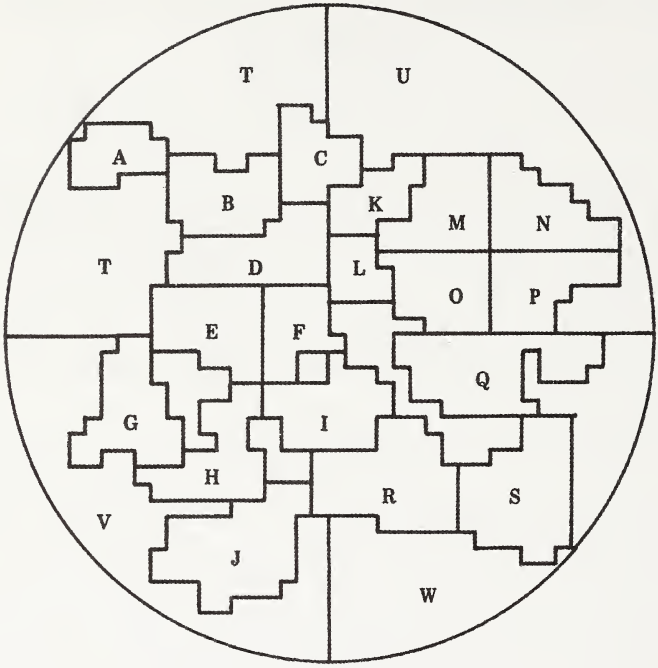

FIGURE 1. West Yorkshire conurbation recording units: the area covered (**A–S** = 607 km², **T–W** = 649 km²) is within a radius of 20 km of grid ref. 44/200.300. For details of recording units see Seaward (1975, 1978).

Each checklist entry provides the following information: (a) current nomenclature (based mainly on Smith *et al.* 2009; Hawksworth 2003), (b) synonym(s) used in earlier publications relating to the WYC lichen flora, (c) first record (collector and/or published source with dates), (d) distribution based on recording units (Figure 1), **A** to **S** within the highly urbanized area and **T** to **W** within 20 km of the centre of WYC, but subjected to a relatively low level of urbanization; records for units within brackets prior to 1967, (e) ecological notes, and where possible status ('extinct' = little chance of returning, and 'extinct?' = some chance of returning or overlooked).

The checklist enumerates 363 taxa (354 species, 1 subspecies, 6 varieties and 2 forms) which are consistently or facultatively lichenized fungi; lichenicolous and non-lichenized fungi, traditionally studied by lichenologists but usually overlooked by mycologists, have not been studied in detail, but the following, for example, are known to occur within the conurbation: *Arthonia phaeophysciae*, *Arthopyrenia punctiformis*, *Arthrorhaphis citrinella*, *Athelia arachnoidea*, *Cyrtidula hippocastani*, *Lichenoconium erodens*, *L. lecanorae*, *L. xanthoriae*, *Mycoporum antecellens*, *Opegrapha parasitica* and *Phaeospora parasitica*. Of the 365 lichen taxa recorded over the past 300 years, 98 are based on old records, the great majority presumed extinct. Of the 268 extant taxa, 149 have been discovered since 1967 when the detailed survey of the conurbation's lichen flora commenced; furthermore, of the extant taxa, 42 are found solely in the highly urbanized areas (**A–S**), 69 are found solely in the essentially rural areas (**T–W**), and 157 are found in both categories.

***Acarospora fuscata* (Schrad.) Th.Fr.** Carrington 1862. **(A),B,(C),D,G,I,K,M,Q / T–W**. On Millstone grit; nitrophilous. Occasional.

***A. glaucocarpa* (Ach.) Körb.** Rotheray 1900. **(T)**. Extinct?

***A. macrospora* (Hepp) A.Massal. ex Bagl.** Shackleton & Hebden 1893. **(A) / (T),V**. On black lime. Rare

***A. rufescens* (Ach.) Kremp.** Miall 1863. **(T)**. Extinct?

***A. smaragdula* (Wahlenb.) A.Massal.** (incl. var. *lesdainii*) Baker 1863. **(A),G,J / T–W**. On Millstone grit. Occasional.

***A. umbilicata* Bagl.** Henderson 1984. **U**. On Millstone grit. Rare.

***A. veronensis* A.Massal.** Shackleton & Hebden 1893. **T**. On Millstone grit; nitrophilous. Rare.

***Acrocordia gemmata* (Ach.) A.Massal.** (syn. *Arthopyrenia alba*) Miall 1863. **(T)**. Extinct?

***Agonimia tristicula* (Nyl.) Zahlbr.** Henderson 2001. **U**. On mosses over stonework. Rare; probably overlooked.

***Amandinea punctata* (Hoffm.) Coppins & Scheid.** (syn. *Buellia punctata*) Carrington 1862. **B,(C),D–G,K–M,Q / T–W**. On wide variety of deciduous trees; nitrophilous. Frequent (rare on siltstone pebbles & Magnesian limestone).

***Anaptychia ciliaris* Körb. ex A.Massal.** Bolton 1775. **(G)**. Extinct.

***Anisomeridium polypori* (Ellis & Everh.) M.E.Barr** Coppins & Seaward 1974. **M / U**. On *Sambucus* and *Ulmus*. Rare.

***Arctoparmelia incurva* (Pers.) Hale** (syn. *Parmelia incurva*) Hebden 1891. **T–V**. On Millstone grit. Uncommon.

***Arthonia didyma* Körb.** (syn. *A. dispersa*) Shackleton 1811. **(T)**. Extinct?

***A. muscigena* Th.Fr.** (syn. *A. leucodontis*) Henderson 1981. **M**. On calcareous sandstone wall-face. Rare.

***A. radiata* (Pers.) Ach.** Shackleton c.1820. **(T),U**. On deciduous trees. Rare.

***Arthrorhaphis citrinella* (Ach.) Poelt** Hitch 1976. **T**. On mortar between siliceous coping stones. Rare.

***Aspicilia caesiocinerea* (Nyl. ex Malbr.) Arnold** (syn. *Lecanora gibbosa*) Bolton 1775. **(G)**. Extinct?

***A. calcarea* (L.) Körb.** (syn. *Lecanora calcarea*) Seaward 1968. **E,M / T,U,W**. On calcareous gravestones, concrete and rockery (? imported stone). Occasional.

***A. cinerea* (L.) Körb.** [s.lat.] (syn. *Lecanora cinerea*) Shackleton c.1820. **(T)**. Extinct?

A. contorta* (Hoffm.) Kremp. ssp. *contorta (syn. *Lecanora contorta*). Seaward 1968. **G,K,M,O / U,W**. On concrete pathways, cement wall-tops and calcareous gravestones. Occasional

***Bacidia arnoldiana* Körb.** Seaward 1981. **B,D,E,G**. On various deciduous trees, mostly *Acer*. Occasional.

***B. caligans* (Nyl.) A.L.Sm.** (syn. *B. 'koerberi'*) Henderson 1976. **Q / U**. On siliceous substrata. Uncommon.

***B. chloroticula* (Nyl.) A.L.Sm.** Henderson 1980. **E,M,P**. On cement aggregate and *Fraxinus*. Rare.

***B. egenula* (Nyl.) Arnold** Earland-Bennett & Henderson 1976. **U**. On siltstone rock by pool. Rare.

***B. rubella* (Hoffm.) A.Massal.** Bohler c.1840. **(C),(J) / (T)**. Extinct?

***B. saxenii* Erichsen** Henderson 1988. **M**. On iron railings. Rare.

***Baeomyces rufus* (Huds.) Rebent.** Bolton 1775. **(B),(C),D,E,G,H,M / T–W**. On Millstone grit and acid soils. Frequent.

***Bilimbia lobulata* (Sommerf.) Hafellner & Coppins** (syn. *Toninia lobulata*) Hebden 1915. **(T)**. Extinct?

***B. sabuletorum* (Schreb.) Arnold** (syn. *Bacidia sabuletorum*) Shackleton & Hebden 1893. **(A),M / T,U,(V),W**. On mosses over calcareous substrata. Occasional.

***Bryoria bicolor* (Ehrh.) Brodo & D.Hawksw.** (syn. *Alectoria bicolor*) Bolton 1775. **(G)**. Extinct.

***B. chalybeiformis* (L.) Brodo & D.Hawksw.** (syn. *Alectoria chalybeiformis*) Hailstone c.1805. **(T)**. Extinct.

***B. fuscescens* (Gyeln.) Brodo & D.Hawksw.** (syn. *Alectoria fuscescens*) Bolton 1775. **(B),(G) / (T),(U)**. Extinct.

***Buellia aethalea* (Ach.) Th.Fr.** Gilbert 1999. **M,S / U,W**. On siliceous gravestones. Occasional.

***B. disciformis* (Fr.) Mudd** Shackleton 1811. **(A)**. Extinct?

***Bunodophoron melanocarpum* (Sw.) Wedin** (syn. *Sphaerophorus melanocarpus*) Nowell c.1862. **(T),(V)**. Extinct.

***Calicium viride* Pers.** Lees 1888. **(V)**. Extinct?

***Caloplaca aurantia* (Pers.) Hellb.** Earland-Bennett 1974. **G**. On asbestos-cement. Rare.

***C. cerina* (Ehrh. ex Hedw.) Th.Fr.** Hailstone c.1805. **(B)**. Extinct.

***C. chlorina* (Flot.) H.Olivier** (syn. *C. isidiigera*) Smith & Henderson 1995. **T,U**. On sandstone. Uncommon.

***C. chrysodeta* (Vain. ex Räsänen) Dombr.** (syn. *Leproplaca chrysodeta*) Hitch 1999. **M**. On calcareous tombstone. Rare.

***C. citrina* (Hoffm.) Th.Fr.** [s.lat. – some records referable to *C. flavocitrina*] Hebden c.1892. **A–S / T–W**. On calcareous substrata. Common.

***C. crenularia* (With.) J.R.Laundon** (syn. *C. ferruginea* var. *festivum*) Carrington 1862. **(T)**. Extinct?

***C. crenulatella* (Nyl.) H.Olivier** Hitch & Henderson 2003. **M**. On calcareous paving. Rare, but overlooked.

***C. decipiens* (Arnold) Blomb. & Forssell** Hebden c.1900. **A,D,K,M / (T),U,W**. On calcareous substrata, especially asbestos-cement. Occasional.

***C. ferruginea* (Huds.) Th.Fr.** Bolton 1775. **(G)**. Extinct.

***C. flavescens* (Huds.) J.R.Laundon** (syn. *C. heppiana*) Bolton 1775. **(G),J,M / U**. On calcareous substrata, especially in churchyards. Occasional.

***C. flavocitrina* (Nyl.) H.Olivier** Hitch *et al.* 1998. **J,M / U**. On calcareous substrata. Occasional, but overlooked.

***C. flavorubescens* (Huds.) J.R.Laundon** (as *C. aurantiaca* p.p.) Bolton 1775. **(G)**. Extinct.

***C. flavovirescens* (Wulfen) Dalla Torre & Sarnth.** (as *C. aurantiaca* p.p.) Rotheray 1900. **(T)**. Extinct?

***C. holocarpa* (Hoffm.) A.E.Wade** [s.lat. – numerous records referable to several taxa, see Smith *et al.* 2009, p.264] Seaward 1968. **A,C–G,I,J,L,M,O,Q,S / T–W**. On calcareous substrata and dusty tree trunks. Frequent.

***C. saxicola* (Hoffm.) Nordin** (syn. *C. murorum*) Lees 1888. **E,J,M / T,(U)**. On calcareous substrata. Occasional.

***C. teicholyta* (Ach.) J.Steiner** Henderson 2001. **U**. On calcareous stonework. Rare.

***C. variabilis* (Pers.) Müll.Arg.** Hebden 1890. **(T)**. Extinct?

***Candelaria concolor* (Dicks.) Stein** Bolton 1775. **(G),(J)**. Extinct?

Candelariella aurella* (Hoffm.) Zahlbr. f. *aurella Hebden 1916. **A–S / T–W**. On calcareous substrata. Common.

f. *smaragdula* Szatala (syn. *C. heidelbergensis*) Henderson 1974. **W**. On asbestos-cement. Rare; probably overlooked.

***C. medians* (Nyl.) A.L.Sm.** Seaward 1968. **A,M / T,U**. On calcareous substrata. Uncommon.

***C. reflexa* (Nyl.) Lettau** Earland-Bennett 1972. **B,E,H,L,M,Q / U–W**. On various deciduous trees. Occasional, but spreading.

***C. vitellina* (Hoffm.) Müll.Arg.** Lees 1888. **A–S / T-W**. On a wide variety of saxicolous substrata, and also on tree bark. Common.

f. *flavovirella* (Nyl.) A.Henderson Henderson 1985. **M**. On sandsone wall coping. Rare.

***Catillaria chalybeia* (Borrer) A.Massal.** Hebden 1916. **(A),B,E,G,H,J,M / T–W**. On

mortar, cement, asbestos-cement and fine-grained sandstone. Occasional, but overlooked.

***C. lenticularis* (Ach.) Th.Fr.** Gilbert & Henderson 1986. **U**. On Millstone grit. Uncommon.

***Cetraria aculeata* (Schreb.) Fr.** (syn. *Cornicularia aculeata*) Hailstone c.1820. **(A),B,(M) / T–V**. On acid soils. Occasional.

***C. islandica* (L.) Ach.** Bolton 1775. **(G)**. Extinct.

***C. muricata* (Ach.) Eckfeldt** (syn. *Cornicularia muricata*) Carrington 1856. **(B) / T,U**. On acid soils. Uncommon.

***Chaenotheca ferruginea* (Turner ex Sm.) Mig.** Coppins & Seaward 1974. **T,U**. On *Quercus*. Rare.

***Chrysothrix candelaris* (L.) J.R.Laundon** Hobkirk 1868. **(V)**. Extinct?

***Cladonia arbuscula* ssp. *squarrosa* (Wallr.) Ruoss** Bolton 1775. **(B),(G) / (T)**. Extinct.

C. cervicornis* (Ach.) Flot. ssp. *cervicornis [some records probably referable to *C. subcervicornis*] Carrington 1862. **(B),D,G / (T),V**. On sandy soil over Millstone grit. Uncommon.

***C. chlorophaea* (Flörke ex Sommerf.) Spreng.** [incl. *C. cryptochlorophaea*] Shackleton & Hebden 1893. **B–I,K,M,N,P,Q,S / T–W**. On acid soils, frequently disturbed, and tree boles. Frequent.

***C. ciliata* var. *tenuis* (Flörke) Ahti** Hebden in Watson 1917 **(A)**. Extinct?

***C. coccifera* (L.) Willd.** [s.lat., most records referable to *C. diversa*] Bolton 1775. **A,B,E,G,H,J,(K),M,Q,R / T–W**. On acid and peaty soils. Locally frequent.

***C. coniocraea* (Flörke) Spreng.** Seaward 1968. **B,D,G,H,K,M,N,P,Q / T–W**. On tree trunks, rotting wood and peaty soils. Locally frequent.

***C. cornuta* (L.) Hoffm.** Henderson 1994. **M**. On industrial wasteland. Rare.

***C. crispata* var. *cetrariiformis* (Delise ex Duby) Vain.** Crosby 1975. **B,H / T,U**. On peaty soils. Uncommon.

***C. digitata* (L.) Hoffm.** Bolton 1775. **(A),B,F,G,M / T,(U),V**. On peaty soils and rotting wood. Occasional.

***C. diversa* Asperges** [most *C. coccifera* records referable to this species] Seaward 1970. **T,V,W**. On acid and peaty soils. Locally frequent; under-recorded.

***C. fimbriata* (L.) Fr.** Bolton 1775. **A–S / T–W**. On a wide variety of substrata in demolition sites, spoil heaps, rockeries, etc. Common.

***C. floerkeana* (Fr.) Flörke** Hebden 1916. **(A),E,G,H,M,Q,R / T-W**. On peaty soils. Locally frequent.

***C. foliacea* (Huds.) Willd.** Bolton 1775. **(G)**. Extinct.

C. furcata* (Huds.) Schrad. ssp. *furcata Bolton 1775. **(A),B,(D),E,G,M,(N) / T,U,(V)**. On acid and peaty soils. Occasional.

***C. glauca* Flörke** Earland-Bennett 1977. **G**. On soil over siltstone wall. Rare.

***C. gracilis* (L.) Willd.** Bolton 1775. **(G) / (T)**. Extinct?

***C. humilis* (With.) J.R.Laundon** (syn. *C. conoidea*, *C. conista*, *C. 'conistea'*) Bolton 1775. **A–C,G,H,J,M,O,Q,S / U,W**. On neutral soils, mainly spoil heaps and disused railway cuttings. Locally frequent.

***C. luteoalba* Wheldon & A.Wilson** Earland-Bennett 1972. **V**. On acid soil. Rare.

***C. macilenta* Hoffm.** (incl. *C. bacillaris* Nyl.) Bolton 1775. **(A),B-H,K,M,Q / T–W**. On peaty and acid soils, and rotting wood. Locally frequent.

***C. ochrochlora* Flörke** [taxonomic status unclear; probably a form of *C. coniocraea*] Hebden c.1894. **(B) / U**. On felled trees. Rare.

***C. pleurota* (Flörke) Schaer.** (syn. *C. coccifera* var. *pleurota*) Earland-Bennett 1972. **T**. On damp peaty soil. Rare.

***C. pocillum* (Ach.) Grognot** Wattam 1913. **M / (V)**. On urban wasteland. Rare.

C. polydactyla* (Flörke) Spreng. var. *polydactyla Bolton 1775. **B,(D),G,M / T–W**. On damp peaty soils and rotting wood. Locally frequent.

***C. portentosa* (Dufour) Coem.** (syn. *C. impexa*) Carrington 1856. **(A),(B),M / T,W**. On

acid soils, including urban wasteland. Occasional.

C. pyxidata **(L.) Hoffm.** [some old records referable to other *Cladonia* species] Bolton 1775. **(B),(G),M,R / T–V**. On dry acid soil. Occasional.

C. ramulosa **(With.) J.R.Laundon** (syn. *C. pityrea*, *C. anomaea*) Earland-Bennett 1973. **(A),M / T**. On soil over Millstone grit. Rare.

C. rangiformis **Hoffm.** Butterfield 1912. **M / (T)**. On urban wasteland. Rare.

C. rei **Schaer.** Earland-Bennett *et al*. 1993. **M**. On urban wasteland. Rare.

C. scabriuscula **(Delise) Nyl.** Butterfield 1912. **(T),U**. On soil. Rare.

C. squamosa **(Scop.) Hoffm. var.** ***squamosa*** Carrington 1856. **(A),B,M,Q / T–V**. On peaty soils. Occasional.

var. ***subsquamosa*** **(Nyl. ex Leight.) Vain.** (syn. *C. squamosa* var. *allosquamosa*) Hebden 1911. **(T)**. Extinct?

C. subcervicornis **(Vain.) Kernst.** Seaward 1972. **T**. On thin soils over Millstone grit. Uncommon.

C. subulata **(L.) F.H.Wigg.** Seaward 1972. **E,G,H,M / T,U,W**. On sandy soils. Occasional.

C. uncialis **ssp.** ***biuncialis*** **(Hoffm.) M.Choisy** Bolton 1775. **(A),(B),(G) / T**. On acid soil. Uncommon.

C. zopfii **Vain.** Carrington 1856. **(T)**. Extinct?

Clauzadea monticola **(Ach.) Hafellner & Bellem.** (syn. *Protoblastenia monticola*) Hebden c.1900. **(A),M / T–V**. On mortar. Occasional

Cliostomum griffithii **(Sm.) Coppins** Hitch *et al*. 1994. **B,G,H / U**. On exposed bases of mature deciduous trees. Occasional.

Collema auriforme **(With.) Coppins & J.R.Laundon** (syn. *C. auriculatum*) Earland-Bennett 1972. **M / T,U**. On limestone and concrete. Uncommon.

C. crispum **(Huds.) F.H.Wigg.** Bolton 1775. **(B),(G),H,M,Q / T,U**. On calcareous substrata. Occasional.

C. cristatum **(L.) F.H.Wigg. var.** ***cristatum*** Bolton 1775. **(G)**. Extinct?

C. fuscovirens **(With.) J.R.Laundon** (syn. *C. tunaeforme*) Lees 1880. **(U)**. Extinct?

C. limosum **(Ach.) Ach.** Hebden 1906. **M,Q / (T),U,(V)**. On soil of derelict site, and paths. Uncommon.

C. tenax **(Sw.) Ach. var.** ***tenax*** Henderson 1976. **(G),M,P / (T),U,(V)**. On various soils and mortar. Occasional.

var. ***ceranoides*** **(Borrer) Degel.** Henderson 1976. **I,M,N,P,Q / T,U**. On compacted soil and amongst mosses on thin soils over asphalt and graves. Occasional, but appears to be increasing.

Collemopsidium monense **(Wheldon) Coppins & Aptroot** (syn. *Pyrenocollema monense*) Henderson 1975. **U**. On mortar. Rare.

Cyphelium inquinans **(Sm.) Trevis.** Lees 1888. **(U)**. Extinct?

Cystocoleus ebeneus **(Dillwyn) Thwaites** (syn. *C. niger*) Seaward & Henderson 1974. **U**. On Millstone grit. Rare.

Dermatocarpon miniatum **(L.) W.Mann** Bolton 1775. **(G)**. Extinct.

Dibaeis roseus **(L.f.) Rambold & Hertel** (syn. *Baeomyces roseus*) Bolton 1775. **(G)**. Extinct?

Dimerella pineti **(Ach.) Vězda** (syn. *D. diluta*) Henderson 1984. **H,M / V,W**. On trunks of *Fraxinus* and *Salix*. Occasional; probably overlooked.

Diploicia canescens **(Dicks.) A.Massal.** (syn. *Buellia canescens*) Seaward 1969. **M**. On limestone memorial. Surprisingly rare; its spread into T-W anticipated due to increased nitrogen-enrichment.

Evernia prunastri **(L.) Ach.** Bolton 1775. **A–F,(G),H,K–M / T–W**. On a wide variety of deciduous trees. Occasional, but spreading since c.1985.

Fellhaneropsis vezdae **(Coppins & P.James) Sérus. & Coppins** Henderson 2001. **U**. On stone urn. Rare.

Flavoparmelia caperata **(L.) Hale** (syn. *Parmelia caperata*) Bolton 1775. **B,(D),E,G,H / T,(U),V,W**. On a variety of deciduous tree trunks. Occasional, but spreading since c.1994.

***F. soredians* (Nyl.) Hale** Seaward 2010. **O**. Single healthy thallus (3.5 cm diam.) on young *Ginkgo biloba* planted here in 2000; it is possible that it came with the tree and has survived, but it is more likely to have colonized it since the replanting. Rare.

Fuscidea cyathoides* (Ach.) V.Wirth & Vězda var. *cyathoides (syn. *Lecidea cyathoides*) Hebden c.1900. **A,G / T,U**. On Millstone grit. Occasional.

***F. praeruptorum* (Du Rietz & H.Magn.) V.Wirth & Vězda** Earland-Bennett 1979. **U,V**. On Millstone grit. Uncommon.

***Graphis elegans* (Borrer ex Sm.) Ach.** Lees 1888. **(K)**. Extinct.

***G. scripta* (L.) Ach.** Bolton 1775. **(G) / (T),(U),(V)**. Extinct?

***Gyalideopsis anastomosans* P.James & Vězda** Gilbert 1988. **U**. On *Acer* and *Salix*. Rare, or overlooked.

Haematomma ochroleucum* (Neck.) J.R.Laundon var. *ochroleucum Bolton c.1775. **(G) / T**. On Millstone grit wall. Rare.

var. *porphyrium* (Pers.) J.R.Laundon Seaward & Coppins 1974. **T,U,W**. On Millstone grit. Occasional.

***Hypocenomyce scalaris* (Ach.ex Lilj.) M.Choisy** (syn. *Lecidea scalaris*) Carrington 1862. **(D) / U**. On dead wood and tree stump. Uncommon.

***Hypogymnia physodes* (L.) Nyl.** (syn. *Parmelia physodes*) Bolton 1775. **A–E,G,H,J,K,M–O / T–W**. On a variety of deciduous trees, mainly *Salix*. Locally frequent; also occasionally on Millstone grit, and rarely on thin peaty soil over spoil heap.

***H. tubulosa* (Schaer.) Hav.** (syn. *Parmelia tubulosa*) Seaward 1969. **B,C,E,G,H,K,M / T–W**. On deciduous trees and Millstone grit. Occasional, but spreading.

***Hypotrachyna revoluta* (Flörke) Hale** (syn. *Parmelia revoluta*) Hitch *et al*. 1995. **E,H,Q / U,W**. On deciduous trees, mainly *Salix*. Occasional, but probably spreading.

***Ionaspis lacustris* (With.) Lutzoni** (syn. *Lecanora lacustris*) Earland-Bennett 1972. **V**. On rocks in streams. Uncommon.

***Lasallia pustulata* (L.) Mérat** (syn. *Umbilicaria pustulata*) Bolton 1772. **(G)**. Extinct.

***Lecania cuprea* (Massal.) Van den Boom & Coppins** Gilbert 2001. **U**. On stone terrace. Rare.

***L. cyrtella* (Ach.) Th.Fr.** Hitch *et al*. 1991. **E,M / U,W**. On a variety of trees. Occasional, but spreading.

***L. erysibe* (Ach.) Mudd** (syn. *L. erysibe* f. *soredíata*) [some older records referable to other *Lecania* species] Hebden 1905. **B,D,E,G–M,Q,S / T–W**. On calcareous substrata. Frequent.

***L. hutchinsiae* (Nyl.) A.L.Sm.** Earland-Bennett 1993. **M**. On base of sandstone wall. Rare, but probably overlooked.

***L. inundata* (Hepp ex Körb.) M.Mayrhofer** Gilbert *et al*. 2001. **U**. On stone terrace. Rare.

***L. nylanderiana* A.Massal.** Henderson 1975. **U**. On mortar. Rare.

***L. subfuscula* (Nyl.) S.Ekman** (syn. *Bacida subfuscula, B.* '*purpurea*') Earland-Bennett 1976. **E,M**. On soil, moss and siliceous stone. Uncommon.

***Lecanora aitema* (Ach.) Hepp** Earland-Bennett 1991. **U**. On wooden seat. Rare.

***L. albescens* (Hoffm.) Branth & Rostr.** Bolton 1775. **(A),B–G,I,J,K–Q,S / T–W**. On calcareous substrata. Locally frequent, but under-recorded.

***L. argentata* (Ach.) Malme** (syn. *L. subfuscata*) Shackleton 1817. **(T)**. Extinct?

L. campestris* (Schaer.) Hue ssp. *campestris Bolton 1775. **D,E,G,M,S / T–W**. On calcareous substrata. Locally frequent.

***L. carpinea* (L.) Vain.** Hitch & Henderson 2005. **O / U**. On twigs and bark of deciduous trees. Rare.

***L. cenisia* Ach.** (as var. *atrynea*) Earland-Bennett 1991. **U**. On wooden seat. Rare.

***L. chlarotera* Nyl.** Bolton 1775. **B,D,G,I,(J),K,M,Q,S / (T),U–W**. On a variety of trees, especially young ones. Occasional, but increasing.

***L. conizaeoides* Nyl. ex Cromb.** Crump & Crossland 1904. **A–S / T–W**. On trees, lignum and acid stone. Formerly ubiquitous, in many places providing a monoculture on

substrata, but now much in decline and found only occasionally, being almost restricted to conifers, lignum and acid gravestones.

***L. crenulata* Hook.** Hebden 1916. **B,J,M / T,U.** On calcareous substrata. Occasional, but under-recorded.

***L. dispersa* (Pers.) Sommerf.** [s.lat.] Shackleton & Hebden 1893. **A–S / T–W.** On calcareous substrata, including dusty tree trunks (*L. dispersa* s.str.), and on trees, decorticate wood and lignum (*L. hagenii*). Common.

***L. epanora* (Ach.) Ach.** Seaward 1970. **E,G / T,V.** On Millstone grit. Occasional.

***L. expallens* Ach.** Wattam 1953. **B–I,K–N,Q,S / T–W.** On deciduous trees and sandstone gravestones. Locally frequent, and spreading.

***L. intricata* (Ach.) Ach.** Earland-Bennett 1972. **G,I,K,M / T.** On Millstone grit. Occasional.

***L. muralis* (Schreb.) Rabenh.** [incl. vars. *albomarginata*, *diffracta* & *versicolor*] Bolton 1775. **A–S / T–W.** On a wide variety of calcareous and non-calcareous substrata, particularly tarmacadam. Common, and spreading, sometimes on the bases of dusty trees.

***L. orosthea* (Ach.) Ach.** (syn. *Lecidea orosthea*) Coppins & Seaward 1974. **U.** On Millstone grit. Rare, but under-recorded.

***L. persimilis* (Th.Fr.) Nyl.** Hitch 2005. **M.** On *Fraxinus*. Rare.

***L. polytropa* (Hoffm.) Rabenh.** Carrington 1862. **A–K,M,O,Q,S / T–W.** On Millstone grit, especially coping stones and gravestones. Frequent.

***L. saligna* (Schrad.) Zahlbr.** Earland-Bennett 1976. **B,D,G,H,M,Q / T,U,W.** On timber. Occasional.

***L. soralifera* (Suza) Räsänen** (syn. *L. intricata* var. *soralifera*) Seaward 1968. **A,B,D,E,G, H,J,K,M / T–V.** On Millstone grit. Frequent.

***L. stenotropa* Nyl.** Seaward 1968. **B,D,E,G–I,K–M,Q / T–W.** On calcareous and non-calcareous substrata. Frequent.

***L. subaurea* Zahlbr.** Earland-Bennett 1971. **G / T,V.** On siltstone walls, mainly coping stones. Occasional.

***L. sulphurea* (Hoffm.) Ach.** (syn. *Lecidea sulphurea*) Seaward 1969. **G,M / T–V.** On Millstone grit. Occasional.

***L. symmicta* (Ach.) Ach.** (syn. *Lecidea symmicta*) Wattam 1953. **Q / U,(V).** On timber. Uncommon.

***L. varia* (Hoffm.) Ach.** [some/all records probably *L. conizaeoides*] Lees 1888. **(T),(U),(V).** Extinct?

***Lecidea fuscoatra* (L.) Ach.** Bolton 1775. **B,(G),J,K,M / T–W.** On siliceous walls and gravestones. Occasional.

***L. hypnorum* Lib.** (syn. *L. templetonii*) Hebden 1916. **(T).** Extinct?

***L. lactea* Flörke ex Schaer.** (syn. *L. pantherina*) Carrington 1862. **(T).** Extinct?

***L. lapicida* (Ach.) Ach.** Carrington 1862. **(C) / (T).** Extinct?

***L. lithophila* (Ach.) Ach.** Shackleton 1818. **(T),(V).** Extinct?

***L. plana* (J.Lahm) Nyl.** Shackleton & Hebden 1893. **(T).** Extinct?

***Lecidella carpathica* Körb.** Earland-Bennett 1974. **G.** On asbestos-cement; building now demolished. Extinct?

L. elaeochroma* (Ach.) M.Choisy f. *elaeochroma (syn. *Lecidea limitata*) Shackleton 1811. **B,E,G,(J),K,L,O, S / (T),U–W.** On twigs and bark of mainly young deciduous trees. Occasional, but spreading.

***L. scabra* (Taylor) Hertel & Leuckert** (syn. *Lecidea scabra*) Hebden 1903. **A–O,Q–S / T–W.** On calcareous and non-calcareous substrata. Locally frequent, rare on timber.

***L. stigmatea* (Ach.) Hertel & Leuckert** (syn. *Lecidea stigmatea*) Hebden c.1892. **A–S / T–W.** On calcareous substrata, especially mortar and asbestos-cement. Frequent.

***Lecidoma demissum* (Rutstr.) Gotth.Schneid. & Hertel** (syn. *Lecidea demissa*) Hebden 1891. **(T).** Extinct.

***Lempholemma polyanthes* (Bernh.) Malme** (syn. *L. chalazanellum, L. chalazanodes*)

Hebden 1916. **(B) / (T)**. Extinct?

***Lepraria caesioalba* (de Lesd.) J.R.Laundon** (syn. *L. zonata, L.* '*neglecta*' p.p.) Earland-Bennett 1972. **G / T–V**. On Millstone grit. Locally frequent.

***L. incana* (L.) Ach.** [s.lat., but most earlier records referable to other *Lepraria* species] Shackleton & Hebden 1893. **A–S / T–W**. On siliceous and calcareous substrata, soil and tree trunks. Common.

***L. lobificans* Nyl.** Hebden c.1905. **M / T**. On various dry substrata. Uncommon, but under-recorded.

***L. vouauxii* (Hue) R.C.Harris** (syn. *Leproloma vouauxii*) Earland-Bennett 1995. **B,C,G,M / T**. On shady stone surfaces shielded from rain. Occasional, but under-recorded.

***Leptogium biatorinum* (Nyl.) Leight.** (syn. *L. pusillum*) Hebden 1906. **H / (T)**. On clay soil of pathway. Rare.

***L. gelatinosum* (With.) J.R.Laundon** Henderson 1993. **B,M / T**. Amongst mosses on calcareous substrata, including urban wasteland. Uncommon.

***L. plicatile* (Ach.) Leight.** Hebden c.1900. **(T),U**. On mortar. Rare.

***L. schraderi* (Ach.) Nyl.** Hebden c.1900. **(T)**. Extinct?

***L. tenuissimum* (Dicks.) Körb.** Hebden 1916. **(T)**. Extinct?

***L. turgidum* (Ach.) Cromb.** Hebden 1889. **(A),B,M,P,Q / (T),U**. On decayed moss and soil on walls and tarmacadam. Occasional.

***Lobaria amplissima* (Scop.) Forssell** Bolton 1775. **(G)**. Extinct.

***L. pulmonaria* (L.) Hoffm.** Bolton 1775. **(G) / (T),(V)**. Extinct.

***L. scrobiculata* (Scop.) DC.** Lightfoot n.d. **(G)**. Extinct.

***L. virens* (With.) J.R.Laundon** (syn. *L. laetevirens*) J.E.Smith n.d. **(G)**. Extinct.

***Megalaria grossa* (Pers. ex Nyl.) Hafellner** (syn. *Catinaria grossa*) Miall 1863. **(T)**. Extinct.

Melanelixia fuliginosa* (Fr. ex Duby) O.Blanco et al. ssp. *fuliginosa (syn. *Parmelia glabratula* ssp. *fuliginosa*) [Bolton 1775 as *P. olivacea* could refer to this and/or the next subspecies, and/or *M. subaurifera*] Wattam 1953. **M / T–W**. On Millstone grit. Occasional.

ssp. *glabratula* (Lamy) O.Blanco et al. (syn. *Parmelia glabratula* ssp. *glabratula*) Wattam 1953. **D,E,G,H,K,L / T–W**. On various deciduous trees. Frequent, probably increasing.

***M. subaurifera* (Nyl.) O.Blanco et al.** (syn. *Parmelia subaurifera*) Seaward 1971. **B–E,G,H,K–N,S / T–W**. On various deciduous trees. Locally frequent, spreading since c.1978.

***Melanohalea exasperata* (De Not.) O.Blanco et al.** (syn. *Melanelia exasperata*) Gilbert 1999. **U,W**. On bark of deciduous tree. Rare.

***M. exasperatula* (Nyl.) O.Blanco et al.** (syn. *Parmelia exasperatula*) Hitch & Henderson 1994. **H**. On bark of deciduous tree. Rare.

***Micarea bauschiana* (Körb.) V.Wirth & Vězda** (syn. *Lecidea semipallens*) Henderson 1976. **T,U**. On siliceous stone. Rare.

***M. botryoides* (Nyl.) Coppins** Henderson 1980. **B,G,H,M / U,V**. On *Acer*, *Alnus* and *Quercus*. Occasional, but overlooked.

***M. denigrata* (Fr.) Hedl.** Henderson 1976. **H,J,M / U–W**. On lignum and tree stumps. Occasional.

***M. erratica* (Körb.) Hertel, Rambold & Pietschm.** (syn. *Lecidea erratica*) Earland-Bennett 1976. **H,M / U**. On siliceous substrata. Uncommon.

***M. lignaria* (Ach.) Hedl.** (syn. *Bacidia lignaria*) Shackleton c.1811. **(A),(C),G / T–W**. On acidic, sometimes mossy, substrata. Occasional.

***M. lynceola* (Th.Fr.) Palice** (syn. *M. excipulata*) Earland-Bennett 1993. **M**. On brick, slate and wood on urban wasteland. Rare.

***M. melaena* (Nyl.) Hedl.** (syn. *Bacidia melaena*) Coppins 1972. **B,G,M / T,U,W**. On tree stumps and decaying wood. Occasional.

***M. peliocarpa* (Anzi) Coppins & R.Sant.** (syn. *Bacidia violacea*) Henderson 1975. **U**. On stone rubble on ditch side. Rare.

***M. polycarpella* (Erichsen) Coppins & Palice** (syn. *Lecidea polycarpella*) Earland-Bennett 1988. **M**. On brick in industrial waste. Rare.

***M. prasina* Fr.** (syn. *Catillaria prasina*) Shackleton & Hebden 1893. **B,G,H,M / T,U**. On *Calluna* and *Ulex*. Occasional, but overlooked.

***M. sylvicola* (Flot.) Vězda & V.Wirth** Earland-Bennett 1977. **T**. On Millstone grit boulder in stream. Rare.

***Miriquidica complanata* (Körb.) Hertel & Rambold** (syn. *Lecanora superiuscula*) Hebden c.1894. **(T)**. Extinct?

***M. leucophaea* (Rabenh.) Hertel & Rambold** (syn. *Lecidea leucophaea*) Earland-Bennett 1971. **T,V**. On siltstone. Uncommon.

***Mycoblastus sanguinarius* (L.) Norman** Bolton 1775. **(B),G,(J),M / T–V,(W)**. On Millstone grit. Occasional.

***Myriospora heppii* Nägeli** (syn. *Acarospora heppii*) Earland-Bennett 1975 **G,M / T–V**. On calcareous substrata. Uncommon.

***Nephroma laevigatum* Ach.** Bolton 1775. **(G)**. Extinct.

***Ochrolechia androgyna* (Hoffm.) Arnold** Seaward 1969. **G,M / T–V**. On Millstone grit; also rarely on tree boles. Locally frequent.

***O. parella* (L.) A.Massal.** (incl. *O. pallescens* p.p.) Carrington 1862. **(G) / (T),U,(V),(W)**. On Millstone grit capstones. Rare.

***O. tartarea* (L.) A.Massal.** Richardson c.1741. **(B),(F),(G) / (V)**. Extinct.

***O. turneri* (Sm.) Hasselrot** Earland-Bennett 1977. **B**. On Millstone grit boulders and exposed roots of *Quercus*. Rare.

***Opegrapha atra* Pers.** Bolton 1775. **(G),(J) / (U),(V)**. Extinct?

***O. calcarea* Turner ex Sm.** (syn. *O. confluens*, *O. saxatilis*) Hobkirk 1868. **(J) / U,(V)**. On shaded base of siliceous wall. Rare.

***O. dolomitica* (Arnold) Clauzade & Cl.Roux** (syn. *O. saxicola*) Lees 1880. **(U)**. Extinct?

***O. rufescens* Pers.** Miall 1863. **(T)**. Extinct?

***O. vulgata* (Ach.) Ach.** Carrington 1862. **(T)**. Extinct?

***Ophioparma ventosa* (L.) Norman** (syn. *Haematomma ventosum*) Bolton c. 1775. **(G) / T**. On Millstone grit. Rare.

***Parmelia discordans* Nyl.** (syn. *P. omphalodes* var. *discordans*) Seaward 1972. **T**. On Millstone grit. Rare, or mistaken for next species.

***P. omphalodes* (L.) Ach.** Bolton 1775. **(A),B,(G) / T,U,(V)**. On Millstone grit. Locally frequent.

***P. saxatilis* (L.) Ach.** Bolton 1775. **A–E,G,H,(J),K,M–O / T–W**. On Millstone grit. Common, rarely on trees.

***P. sulcata* Taylor** Seaward 1969. **A,B,D–N,Q / T–W**. On deciduous trees, mainly *Acer*, *Fraxinus* and *Salix*, lignum and siliceous walls. Common, and increasing on tree trunks.

***Parmeliopsis ambigua* (Wulfen) Nyl.** Earland-Bennett 1972. **T,V**. On Millstone grit. Uncommon.

***P. perlatum* (Huds.) M.Choisy** (syn. *Parmelia perlata*) Bolton 1775. **B,E,(G),M / T,U,(V)**. On trees, mainly *Salix*. Formerly extinct, but returning since the late 1990s.

***Peltigera didactyla* (With.) J.R.Laundon** (syn. *P. spuria*) Hebden 1914. **H,K,M,N / T–V**. On clayey soil of spoil tips and waste ground; also on disused railway tracks. Occasional.

***P. horizontalis* (Huds.) Baumg.** Bolton 1775. **(B),(G) / (T)**. Extinct.

***P. hymenina* (Ach.) Delise ex Duby** (syn. *P. "polydactyla"*) Carrington 1862. **(A),(B),(C),F–H,K,P / T**. On clayey soil, sometimes in lawns. Occasional.

***P. membranacea* (Ach.) Nyl.** [as *P. canina* s.lat.; possibly this or other *Peltigera* spp.] Bolton 1775. **(B),(G) / (T),(U),(V)**. Extinct?

***P. praetextata* (Flörke ex Sommerf.) Zopf** Watson 1946. **(T)**. Extinct.

***P. rufescens* (Weiss) Humb.** Crump & Crossland 1904. **M / (T)**. On urban wasteland. Rare.

Pertusaria albescens* (Huds.) M.Choisy & Werner var. *albescens Bolton 1775. **(G)**. Extinct?

var. *corallina* (Zahlbr.) J.R.Laundon Seaward & Henderson 1974. **U**. On Millstone grit capstone. Rare.

***P. amara* (Ach.) Nyl.** Bolton 1775. **(G) / (T),(V)**. Extinct?

***P. corallina* (L.) Arnold** Carrington 1862. **T,U,W**. On Millstone grit. Occasional.

***P. leioplaca* DC.** Shackleton 1817. **(A)**. Extinct.

***P. pertusa* (Weigel) Tuck.** Bolton 1775. **(G) / (U),(V)**. Extinct?

***Phaeophyscia nigricans* (Flörke) Moberg** (syn. *Physcia nigricans*) Seaward 1970. **G,K,M / T,U,W**. On calcareous substrata, mainly asbestos-cement. Occasional; rare on dusty tree trunks.

***P. orbicularis* (Neck.) Moberg** (syn. *Physcia orbicularis*) Carrington 1862. **A–S / T–W**. On calcareous substrata, deciduous trees and lignum; spreading on trees due to nitrogen-enrichment. Common.

***Phlyctis argena* (Spreng.) Flot.** Smith & Henderson 1995. **U**. On sandstone wall. Rare.

***Physcia adscendens* (Fr.) H.Olivier** Seaward 1968. **A–S / T–W**. On calcareous substrata and deciduous trees; spreading on trees due to nitrogen enrichment. Common.

***P. aipolia* (Ehrh. ex Humb.) Fürnr.** Henderson 2001. **U**. On orchard tree. Rare.

***P. caesia* (Hoffm.) Fürnr.** Hebden 1909. **A–S / T–W**. On calcareous substrata and dusty trees; nitrophilous. Frequent, spreading onto trees since c.1990.

***P. dubia* (Hoffm.) Lettau** Earland-Bennett 1972. **G / T–V**. On nutrient-enriched or dust impregnated siliceous stonework, timber and trees. Occasional.

***P. stellaris* (L.) Nyl.** Bolton 1775. **(G),L**. Several thalli on two *Acer*. Rare.

***P. tenella* (Scop.) DC.** Bolton c. 1775. **A–S / T–W**. On deciduous trees and lignum, particularly if nitrogen-enriched; also on calcareous substrata. Common, spreading.

***Physconia grisea* (Lam.) Poelt** (syn. *Physcia grisea*) West 1882. **(B),(D),G,M / U,W**. On calcareous substrata and deciduous trees. Occasional, spreading on trees.

***Placynthiella dasaea* (Stirt.) Tønsberg** Earland-Bennett 1993. **B,G,M**. On lignum and rotting wood. Uncommon, but overlooked.

***P. icmalea* (Ach.) Coppins & P.James** Seaward 1985. **B–D,G,H,J,K,M,P / T–W**. On lignum and rotting wood. Frequent.

***P. uliginosa* (Schrad.) Coppins & P.James** (syn. *Lecidea uliginosa*) Carrington 1862. **A,B,D,E,G,H,O–S / T–W**. On peaty soils and dead wood. Locally frequent.

***Placynthium nigrum* (Huds.) Gray** Lindsay 1859. **(A),(B),(C),M / U**. On calcareous stones. Occasional.

***Platismatia glauca* (L.) W.L.Culb. & C.F.Culb.** (syn. *Cetraria glauca*) Bolton 1775. **B,G,H,K / T–W**. On Millstone grit and acid-barked trees. Occasional.

***Polyblastia albida* Arnold** Shackleton & Hebden. **(A) / (T)**. Extinct?

***P. cupularis* A.Massal.** Rotheray 1900. **(T)**. Extinct?

***Polysporina simplex* (Davies) Vězda** Earland-Bennett 1976. **K / T,U,W**. On siliceous substrata. Occasional.

***Porina chlorotica* (Ach.) Müll.Arg.** Henderson & Hackett 1985. **M / U**. On sandstone. Uncommon.

***Porpidia cinereoatra* (Ach.) Hertel & Knoph** (syn. *Lecidea* '*albocaerulescens*') Seaward 1970. **A,D,G,M / T–V**. On Millstone grit. Locally frequent.

***P. crustulata* (Ach.) Hertel & Knoph.** (syn. *Lecidea crustulata*) Carrington 1862. **(C),I,K / T–W**. On siliceous substrata. Occasional.

***P. hydrophila* (Fr.) Hertel & A.J.Schwab** (syn. *Lecidea hydrophila*) Shackleton & Hebden 1893. **(T)**. Extinct?

***P. macrocarpa* (DC.) Hertel & A.J.Schwab** (syn. *Lecidea macrocarpa*) West 1881. **A,(B),D,G,K,M / T–W**. On Millstone grit. Locally frequent.

***P. platycarpoides* (Bagl.) Hertel** Earland-Bennett 1993. **M**. On sandstone pebble amongst industrial waste. Rare.

***P. soredizodes* (Lamy ex Nyl.) J.R.Laundon** Hitch *et al.* 1991. **B,I,K,M / T–V**. On

siliceous substrata. Locally frequent.

***P. tuberculosa* (Sm.) Hertel & Knoph** (syn. *Lecidea tumida*) Hebden 1916. **A–S / T–W**. On siliceous substrata. Frequent.

***Protoblastenia calva* (Dicks.) Zahlbr.** (syn. *P. rupestris* var. *calva*) Wattam 1953. **(J)**. Extinct?

***P. rupestris* (Scop.) J.Steiner** Hebden 1891. **D,M / T–V**. On mortar. Occasional.

***Protoparmelia badia* (Hoffm.) Hafellner** (syn. *Lecanora badia*, incl. var. *cinerascens*, *L. picea*) Carrington 1892. **(A),(C) / T,U**. On Millstone grit. Uncommon.

***P. nephaea* (Sommerf.) R.Sant.** (syn. *Lecanora nephaea*) Shackleton & Hebden 1893. **(T)**. Extinct?

***Pseudevernia furfuracea* (L.) Zopf** [s.lat., i.e. vars. *furfuracea* & *ceratea*] Bolton 1775. **(B),(G) / T–V**. On Millstone grit. Locally frequent.

var. *furfuracea* (syn. *Parmelia furfuracea* var. *furfuracea*) Hebden c.1900. **(T)**. Extinct?

var. *ceratea* (Ach.) D.Hawksw. (syn. *Parmelia furfuracea* var. *ceratea*) Seaward 1968. **T–V**. On Millstone grit. Locally frequent.

***Psilolechia leprosa* Coppins & Purvis** Smith & Henderson 1995. **U–W**. On copper-enriched church walls. Occasional

***P. lucida* (Ach.) M.Choisy** (syn. *Lecidea lucida*) Seaward 1968. **A,B,D,G,H,M,O,Q,S / T–W**. On shady non-calcareous walls. Frequent.

***Punctelia subrudecta* (Nyl.) Krog** [s.lat. – i.e. *P. subrudecta* s.str. and/or *P. jeckeri*] Hitch & Henderson 1994. **H,Q / T,U,W**. On deciduous trees. Occasional, but spreading since the late 1990s.

***P. jeckeri* (Roum.) Kalb** (syn. *P. ulophylla*) Dalrymple 2001. **E**. On deciduous trees. Rare, but probably overlooked (see previous entry).

***Racodium rupestre* Pers.** Hebden 1911. **(A),(B) / (T),(V)**. Extinct?

***Ramalina calicaris* (L.) Fr.** Bolton 1775. **(G)**. Extinct.

***R. farinacea* (L.) Ach.** Bolton 1775. **B–E,G,H,K,M,N / T–W**. On a wide variety of deciduous trees. Locally frequent, spreading since c.1977.

***R. fraxinea* (L.) Ach.** Bolton 1775. **(G)**. Extinct.

***Rhizocarpon distinctum* Th.Fr.** Shackleton & Hebden 1893. **(T),U,V**. On siliceous substrata. Uncommon.

***R. geographicum* (L.) DC.** Bolton 1775. **(A),G / T–V**. On Millstone grit. Occasional.

***R. lavatum* (Fr.) Hazsl.** Earland-Bennett 1975. **V**. On gritstone boulder in stream. Rare.

***R. oederi* (Weber) Körb.** Bolton c.1775. **(G) / T**. On Millstone grit. Rare.

***R. petraeum* (Wulfen) A.Massal.** (syn. *R. concentricum*) Rotheray 1900. **T–V**. On calcareous and siliceous (influenced by mortar) substrata. Occasional.

***R. reductum* Th.Fr.** (syn. *R. obscuratum*) Hebden 1916. **B–D,G,H,K,M,S / T–W**. On siliceous substrata. Locally frequent.

***R. viridiatrum* (Wulfen) Körb.** Hebden 1916. **(T)**. Extinct.

***Rinodina oleae* Bagl.** (syn. *R. subexigua*, *R. gennarii*, *R. exigua* p.p.) Seaward 1968. **A,C–E,G–Q,S / T–W**. On calcareous substrata and lignum; nitrophilous. Frequent.

***R. pityrea* Ropin & H.Mayrhofer** Earland-Bennett *et al.* 1995. **G**. On nutrient-enriched bark. Rare.

***R. teichophila* (Nyl.) Arnold** Smith & Henderson 1995. **I**. On sandstone wall. Rare.

***Sarcogyne privigna* (Ach.) A.Massal.** Smith 1996. **T**. On sandstone. Rare

***S. regularis* Körb.** Shackleton & Hebden 1893. **(A),D,G,J,K,M,Q / T–W**. On calcareous substrata, particularly mortar. Frequent.

***Sarcopyrenia gibba* var. *geisleri* (Beckh.) Nav.-Ros. & Hladun** Smith & Henderson 1995. **B,I,L / U**. On memorial stones. Uncommon.

Sarcosagium campestre* (Fr.) Poetsch & Schied. var. *campestre Henderson 1993. **M**. On industrial waste. Rare.

***Scoliciosporum chlorococcum* (Graewe ex Stenh.) Vězda** (syn. *Bacidia chlorococca*)

Seaward 1969. **A,B,D,G,H,M,O,Q / T–W**. On *Salix*, in branch axils; also on *Calluna*, *Rosa* and *Vaccinium*. Occasional, but overlooked.

***S. umbrinum* (Ach.) Arnold** (syn. *Bacidia umbrina*) Seaward 1970. **A,E,G,H,J,K,L–Q,S / T–W**. On calcareous substrata, particularly concrete. Frequent.

***Solorina saccata* (L.) Ach.** Bolton 1775. **(G) / (U)**. Extinct.

***S. spongiosa* (Ach.) Anzi** Hebden 1906. **(T)**. Extinct.

***Sphaerophorus fragilis* (L.) Pers.** Bolton 1775. **(B),(G) / (T),(V)**. Extinct.

***S. globosus* (Huds.) Vain.** Bolton 1775. **(G) / (V)**. Extinct.

***Stereocaulon condensatum* Hoffm.** Hebden 1916. **(A) / (T)**. Extinct.

***S. dactylophyllum* Flörke** Bolton 1775. **(G) / T**. On siliceous outcrop. Rare.

***S. evolutum* Graewe** Hebden 1910. **(T)**. Extinct.

***S. pileatum* Ach.** Wattam 1914. **D,E,H,J / T,U,(V),W**. On siliceous substrata. Occasional.

S. vesuvianum* Pers. var. *vesuvianum Seaward 1968. **B,D,G,H,J / T–V**. On Millstone grit. Locally frequent.

***Sticta limbata* (Sm.) Ach.** Hebden 1906. **(T)**. Extinct.

***S. sylvatica* (Huds.) Ach.** Bolton 1775. **(G)**. Extinct.

***Strangospora moriformis* (Ach.) Stein** Henderson 1975. **B,D / U**. On *Acer* and lignum. Uncommon.

***S. pinicola* (A.Massal.) Körb.** Earland-Bennett 1976. **E,G,M,Q / T**. On exposed bark of deciduous trees. Occasional.

***Teloschistes flavicans* (Sw.) Norman** Bolton 1775. **(G)**. Extinct.

***Tephromela atra* (Huds.) Hafellner ex Kalb** (syn. *Lecanora atra*) Bolton 1775. **(C),(D),(G),M / (T),U,(V)**. On Millstone grit. Occasional.

var. *torulosa* (Flot.) Hafellner Bohler c.1840. **(J)**. Extinct.

***Thelidium decipiens* (Nyl.) Kremp.** Henderson 2001. **M / U**. On calcareous substrata. Uncommon.

***T. impressum* (Stizenb.) Zschacke** Earland-Bennett 1976. **V**. On mortar. Rare.

***T. incavatum* Mudd** Hebden 1891. **M / T,U**. On mortar. Uncommon.

***T. minutulum* Körb.** (syn. *T. mesotropum*) Coppins & Seaward 1974. **M,P / U**. On weakly calcareous stones. Occasional.

***T. zwackhii* (Hepp) A.Massal.** Earland-Bennett 1992. **M**. On soil of derelict site; now extinct.

***Thelocarpon laureri* (Flot.) Nyl.** Gilbert 1988. **P**. On demolition site. Rare.

***Toninia aromatica* (Sm.) A.Massal.** Rotheray 1900. **T,U,(V)**. On calcareous substrata. Uncommon.

***Trapelia coarctata* (Sm.) M.Choisy** (syn. *Lecidea coarctata*) Shackleton 1814. **A–Q,S / T–W**. On siliceous substrata. Frequent.

***T. glebulosa* (Sm.) J.R.Laundon** (syn. *T. involuta*, *Lecidea coarctata* var. *ornata*) Seaward 1969. **G,K,M / T–W**. On Millstone grit. Locally frequent.

***T. obtegens* (Th.Fr.) Hertel** Earland-Bennett 1976. **E,G,J,K,M,R / T–V**. On siliceous substrata. Frequent.

***T. placodioides* Coppins & P.James** Seaward 1986. **C,G,H–J,M,N,S / T–W**. On smooth siliceous substrata. Locally frequent.

***Trapeliopsis flexuosa* (Fr.) Coppins & P.James** (syn. *Lecidea aeruginosa*) Henderson 1980. **G,M / U,V**. On wood. Occasional.

***T. gelatinosa* (Flörke) Coppins & P.James** (syn. *Lecidea gelatinosa*) Shackleton & Hebden 1893. **(T)**. Extinct?

***T. granulosa* (Hoffm.) Lumbsch** (syn. *Lecidea granulosa*) Carrington 1862. **A–S / T–W**. On decaying wood and acid soils. Common.

***T. pseudogranulosa* Coppins & P.James** Seaward 1985. **T,U**. On peaty soil and decaying plant debris. Uncommon.

***Tuckermanopsis chlorophylla* (Willd.) Hale** (syn. *Cetraria chlorophylla*) Seaward 1968. **T**. On Milstone grit. Rare.

***Umbilicaria polyphylla* (L.) Baumg.** Bolton 1775. **(B),(G) / (T)**. Extinct?

***U. polyrrhiza* (L.) Fr.** Bolton 1775. **(G) / T**. On Millstone grit. Rare.
***U. proboscidea* (L.) Schrad.** Bolton 1775. **(G)**. Extinct.
***U. torrefacta* (Lightf.) Schrad.** Bolton 1775. **(G)**. Extinct.
***Usnea articulata* (L.) Hoffm.** Bolton 1775. **(G)**. Extinct.
***U. filipendula* Stirt.** Bolton 1775. **(G)**. Extinct.
***U. florida* (L.) F.H.Wigg.** Bolton 1775. **(B),(G)**. Extinct.
***U. hirta* (L.) F.H.Wigg.** Bolton 1775. **(G)**. Extinct.
***U. subfloridana* Stirt.** Seaward 1972. **B,E,H,M / T–V**. On deciduous trees; small thalli which are often short-lived. Occasional, but spreading since 1991.
***Verrucaria aquatilis* Mudd** Earland-Bennett 1974. **W**. On siliceous rocks at edge of lake. Rare.
***V. baldensis* A.Massal.** (syn. *V. sphinctrina*) Seaward 1969. **D,M / T,U,W**. On calcareous substrata. Occasional.
***V. bryoctona* (Th.Fr.) Orange** Gilbert 1988. **P**. On demolition site. Rare.
***V. dolosa* Hepp** (syn. *V. mutabilis* p.p.) Rotheray 1900. **M / (T)**. On industrial waste. Rare.
***V. elaeina* Borrer** Hitch & Henderson 2003. **M**. On marble. Rare.
***V. elaeomelaena* (A.Massal.) Arnold** Hebden 1902. **G / (T),U**. On siliceous boulder in stream. Rare.
***V. hochstetteri* Fr.** Seaward 1969. **D,E,G,M / T–W**. On calcareous substrata, particularly mortar. Occasional, but overlooked.
***V. hydrela* Ach.** Shackleton & Hebden 1893. **(T),U**. On siliceous stone in stream. Rare.
***V. macrostoma* Dufour ex DC.** [incl. f. *furfuracea* de Lesd. (syn. *V. viridula* f. *tectorum*)] Shackleton & Hebden 1892. **A,B,I,L,O,M / T–W**. On calcareous substrata, sometimes nutrient-enriched. Frequent.
***V. margacea* (Wahlenb.) Wahlenb.** Shackleton 1810. (T). Extinct?
***V. muralis* Ach.** Hebden 1889. **A–S / T–W**. On calcareous substrata. Common.
***V. murina* Leight.** Henderson 1974. **R**. On concrete. Rare.
***V. nigrescens* Pers.** Seaward 1969. **A–S / T–W**. On calcareous (and occasionally siliceous) substrata. Common.
***V. praetermissa* (Trevis.) Anzi** Earland-Bennett 1977. **T**. On quartzite boulder in stream. Rare.
***V. viridula* (Schrad.) Ach.** Hebden c.1900. **A,B,F,I,K–O,Q,S / T–W**. On calcareous substrata, occasionally nutrient-enriched. Common.
***Vezdaea leprosa* (P.James) Vězda** Henderson 1993. **M**. On industrial metalliferous waste. Rare.
***V. retigera* Poelt & Döbbeler** Earland-Bennett 1993. **M**. On cloth in urban wasteland. Rare; probably extinct.
***Vulpicida pinastri* (Scop.) Mattson & M.J.Lai** (syn. *Cetraria pinastri*) Bolton 1775. **(G)**. Extinct.
***Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale** (syn. *Parmelia conspersa*) Bolton 1775. **(G),(J) / (T),(V)**. Extinct?
***X. mougeotii* (Schaer. ex D.Dietr.) Hale** (syn. *Parmelia mougeotii*) Carrington 1862. **(T),(U)**. Extinct?
***Xanthoria calcicola* Oxner** (syn. *X. aureola* auct. brit.) Seaward 1969. **G,M,N / T–V**. On calcareous substrata; nitrophilous. Locally frequent.
***X. candelaria* (L.) Th.Fr.** Seaward 1970. **B–F,H,I,K–N,Q,S / T–W**. On deciduous trees, mainly *Acer* and *Fraxinus*; nitrophilous. Frequent, and spreading.
***X. elegans* (Link) Th.Fr.** Seaward 1970. **B,G,M / T–V**. On concrete and asbestos-cement. Occasional.
***X. parietina* (L.) Th.Fr.** Bolton 1775. **A–S / T–W**. On calcareous substrata and tree; nitrophilous. Common, and spreading.
***X. polycarpa* (Hoffm.) Th.Fr. ex Rieber** Seaward 1985. **B,D,E,H–M,P,Q,S / T–W**. On a variety of deciduous trees; nitrophilous. Frequent, and spreading.
***X. ucrainica* S.Y.Kondr.** Henderson & Hitch 2003. **M**. On *Fraxinus*. Rare.

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BOOK REVIEWS

Photographing Pattern & Design in Nature. A Close-up Guide by **Arnold Wilson**. Pp.144, with numerous full colour illus. A & C Black. 2010. £19.99 paperback.

This inspiring 'Close-up' guide contains wonderful images of detail and pattern in nature. The camera is a tool: it is the experience and talent of the photographer that creates a good composition. Looking first through Arnold Wilson's portfolio (the large pictures at the back of the book), you can enjoy the beauty, colours and complexity of design in bark, feathers, butterfly wings, lichens and leaves. Then you can find how these images were captured.

The text, clear diagrams and examples inspire you to rush out into your garden/nearest park and experiment with your camera and some props, or to collect pine cones, leaves, a flower for an indoor shoot. You may not have thought of using a background board, mirror (to reflect sunlight for side or back-lighting for a 3D effect). Practical advice includes avoiding harsh light/windy weather; trying out high/low angles; keeping camera and spare

batteries warm, next to your body on cold days – or before entering a Tropical House, to avoid misting up the lens! More people now have Super Macro (flower mode) on their digital cameras. It is exciting to set your camera on superfine setting, to move in closer where possible and take pictures. Then when you see the results on your computer screen/print, you can discover and delight in the detail of symmetry, structure and textures – not obvious to the naked eye. This book will certainly help you to create better pictures.

VC & ZC

The Life and Love of Trees by **Lewis Blackwell**. Pp. 201. Chronicle Books. 2010. £35.00 hardback.

A coffee table tree feast is Blackwell's product in this heavily formatted book, designed to set up a four-part harmony: bare paper for us to begin thinking, uncredited quotes, and blocks of tiny text draw us into his tour of the world's photo libraries.

In relegating his sources for both quotes and images to the back covers, Blackwell keeps us wondering whether or not he's just made up the words, or if they are from some reputable source. He makes us look really deep into the pictures without needing to be curious about the particulars.

Clearly, the blocks of text are intended to be read either on the second or third run through, or not at all. Pitching the maxims in the middle of fields, or in acres of blank space, is supposed to make them weightier, but instead invites scepticism of their false gravitas. At worst, reminders of shallow religious posters spring to mind. The barcode chapter headings simply kill the flow of the book. Much of the narrative is too chatty, and the opportunity has been lost to add prose to the wonderful images, Blackwell here choosing his words to add the light touch.

Gathering thoughts and breathing between the stunning pictures is the strength of this fashion-forced design. Extended perspectives are followed by a humbling sequence of worm's eye views. Similar compositions of differing forests and continents group the reader's thoughts. Bark, bud, leaf, root, flower and seed fill out exquisite details. It's a great, over-edited book, once the reader tunes in, and adheres to the instructions.

HC

Darwin in Galapagos. Footsteps to a New World by **K. Thalia Grant** and **Gregory B. Estes**. Pp. xiv + 362 (incl. 3 maps), plus 64 pages of b/w & full colour plates. 2009. Princeton University Press, Princeton & Oxford. £20.95 hardback.

Although Darwin spent only five weeks in Galapagos, a very small fraction of his 248-week voyage on HMS *Beagle*, his observations there were to have a profound, indeed crucial, impact upon his subsequent thinking. During his stay on Galapagos (15 Sept. – Oct. 1835) he explored the fauna, flora and geology of four of its islands, hiking 50 miles and amassing c. 500 specimens. However, it should be noted that the evidence he assembled for his theories was not derived mainly/solely on the basis of his stay on Galapagos, for his voyages to/from these islands were also highly fortuitous in exposing the young scientist to a wealth of geological and biological evidence.

The authors retrace Darwin's expeditions, meticulously cross-referencing his investigations to original and subsequent documents, correspondence and publications. In fact, the "footnotes" extend to over 77 pages (however, judicious use of abbreviations for titles and authors could have considerably reduced its length). The publishers are to be congratulated on the excellence of this production, more particularly their choice of illustrations, as are the authors for assessing the relative importance of Darwin's extensive observations and discoveries on Galapagos.

MRDS

A NATURALIST IN WARTIME: JOHN BUXTON'S PIONEERING STUDY OF THE REDSTART

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When John Buxton described himself in correspondence, he claimed first and foremost to be a poet. Indeed, during most of his life he held a position as lecturer in English at New College, Oxford, specializing in the 16th and 17th centuries. He published widely in the field, and was perhaps best known for his books, *Sir Philip Sidney and the English Renaissance* and *Elizabethan Taste*. Ornithologists, however, remember Buxton for his meticulous study of redstarts, researched whilst a prisoner in Germany during the Second World War (Snow, 1990a). As a result of this work, contemporaries ranked Buxton as one of the leading naturalists among those amateurs who – though "not trained professionals in the strict sense of the word" – made significant contributions to scientific ornithology (Tinbergen, 1959: 129). In obituaries for *The Times* and the ornithological journal *The Ibis*, he was referred to as "the last amateur ornithologist" (Snow, 1990b).

When writing about birds Buxton himself repeatedly emphasized that he was "of course no expert". Although the claim often seemed to contain more sarcasm than modesty (Buxton did not think "expert" knowledge was necessarily better), the new group of professional ornithologists reforming the discipline in the 1940s and 1950s found in Buxton's careful attention to the life history of a single species an ideal monograph. "Expert" or not, Buxton's work on redstarts provided a wonderful example of the continued importance of amateurs in the history of ornithology and natural history more generally. It also serves as an eloquent example of how detailed attention to natural history allowed at least a few individuals to pass otherwise monotonous days as prisoners of war. Like so many naturalists, they found solace from traumatic times through following in the footsteps of Gilbert White.

BIRDS AND WAR

Edward John Mawby Buxton was born at Bramhall in Cheshire on 16 December 1912. He began watching birds as a schoolboy, and continued doing so throughout his life, always keeping meticulous records. From public school at Malvern College he went on to New College, Oxford, where he read Greats, wrote poetry, and demonstrated an interest in archaeology. David Snow gave a brief description of his character in his obituary in *The Ibis*: "Strongly built, darkly handsome, broad-browed, and intelligent, John Buxton was an impressive figure. He was usually quiet but at times abrupt and even abrasive, and uncompromising over matters of principle". I leave the last word to Peter Conder: "Did not suffer fools gladly. A snort of contempt was characteristic. But he was enormously helpful to all kinds of people" (Snow, 1990a: 621).

At the age of 27, Buxton married Marjorie Lockley, sister to the well-known nature writer Ronald Lockley who had been instrumental in setting up the first bird observatories in Britain (described in Allen, 1976). After travelling to Heligoland to see the 'Heligoland Trap' in 1933, Lockley set up his own trap on the island of Skokholm; Buxton helped him with this work (Lockley, 1947:181), and during their trips he made observations of his own on the breeding of oystercatchers which he prepared for publication in *British Birds*. World events inspired him to submit this work in 1939, earlier than he would otherwise have done: "I had hoped to make this paper more complete by further observations" he wrote, "but in the present uncertain circumstances I have thought best to publish it now" (Buxton, 1939: 193).

He thought wisely. His knowledge of Norwegian destined him for a position as an officer to the 1 Independent Company (later 1 Commando) in Norway as soon as war broke

out. "I hope you'll find time to write me a letter or two while I'm being a soldier", he wrote to a friend just prior to leaving, "I'm not a soldier, and I want to hold hard to as much of the real life – New College, Norway, poetry, birds, wandering about hills and forests on ski and foot, and the sea - as I can. The other is only a nightmarish interlude. I may wake up, or I may not – that doesn't worry me. The thing is that someone should wake up".[1]

In June of 1940, Buxton disappeared while taking part in the attempt to stem the German invasion of Norway (Snow, 1990a: 621). Lockley had been writing to Buxton about the natural history of the island of Skokholm since September 1939 and recorded hearing of his capture:

> "This nightmare war! I was sitting down to write you a letter about migration when the fishing-boat arrived in the harbour with a letter from Marjorie with the message that you are reported missing in Norway. I was stunned with the news, and for a while, my dear John, I must confess I sat with a mist of tears before my eyes. The letter had been difficult to read, for it was already beautifully stained with the tears of the anguished woman who wrote it. But there it was, on re-reading it the letter told me without any doubt that you were reported missing" (Lockley, 1947: 141).

Five days later Marjorie and Lockley learned that Buxton had been taken, unwounded, as a prisoner of war. Lockley kept writing to him, certain that his position as an officer would ensure relatively good treatment and access to post from home. He subsequently published these letters as a group of essays on the natural history of Skokholm. Perhaps they first gave Buxton the inspiration to attempt a natural history study while interned, for Lockley wrote: "You will no doubt deeply regret the circumstances that have resulted in your imprisonment. But these were beyond your control, and must be accepted with the philosophy with which your mind, as I well know, is fully equipped ... In your prison camp you will no doubt, as an officer, have some if not much leisure in which to think and read and write. You will in a sense be as enisled [sic] as we are, and your observations will be limited to the fauna of that entity of your camp and its perimeter. This should give you the chance of concentrating particularly on one or two species as I have done here, and making a study of great interest" (Lockley, 1947: 144).

Buxton spent the rest of the war as a prisoner in various camps in Germany. During this time, under conditions of confinement and surveillance, he observed the breeding behaviour of redstarts. As he wrote some years later, he chose his subject carefully, in consideration of his situation and abilities: "The naturalist who is confined by the barbed wire of a German prison camp to a few acres crowded with humanity must consider carefully before he decides what is to be the subject of his study. He must take account of his own limitations – lack of apparatus such as field glasses, camera, or microscope, lack of a reference library, very likely of notebooks as well; above all the maddening restriction on his movements so that he must wait till the animal he has chosen to study visits him, and cannot follow it round the corner or past that bush. Further, he may hope to find some fellow-prisoners willing or eager to learn: he must then choose some species that is readily identified. Clearly then the easiest creatures for a prisoner to watch are birds, mammals with their nocturnal habits are obviously unsatisfactory. Birds are at once delightful and easy to watch. Most of them go to bed at night like any Christian; many confine themselves voluntarily to an area which with luck may fit inside a prison camp. They do not live under beds or in other suspicious places, and, though the climbing of trees was rather discouraged, enough could usually be seen without that" (Buxton, 1945).

By the end of his imprisonment, Buxton had observed, in varying but always meticulous detail, four pairs of redstarts, three in 1941 in Laufen and one in 1943 at Eichstätt, both in Bavaria. In 300 pages of notes in small print he recorded each bird's activities. Brief summaries at the end of the day gave more general observations. He tallied the total number of hours of observations on a slip of paper placed at the end of his notebook: 839 hours from April 1st to the end of September for one pair.[1] His situation as a prisoner of war created various advantages few naturalists in Britain could boast, most importantly more leisure than he could ever have desired. But for a naturalist who wished

to make a complete, reliable record of the life of a pair of animals, being in a prisoner-of-war camp had its own peculiar disadvantages. Searches and library checks occasionally prevented observations, and Buxton's activities aroused the suspicion of the guards, who sometimes confiscated his notes and forbade early watches at the camp at Eichstätt (Buxton, 1950: 144). At first the guards believed the day-long watches on the pair of redstarts to be a ruse to map the country beyond for a mass escape ("Birds gave solace to caged men", *News Chronicle*, 20 March 1950). However, Buxton eventually convinced his captors that his amusement was harmless, and they even permitted him to erect nest boxes, encouraging the birds to nest within an easier distance.

When his endeavour aroused the interest of some of his fellow inmates, Buxton recruited them to aid him with the long hours of observation; sixteen men helped with the "sometimes tedious task". At various times experienced birdwatchers were interned in the same camp, including Peter Conder, George Waterston, and Dick Purchon, some of whom Buxton had met in the field at bird observatories prior to the war. The most productive camp for natural history studies proved to be the one at Eichstätt, where Waterston studied nesting wrynecks, Conder studied goldfinches, Purchon observed nestling swallows, and George Raeburn watched red-backed shrikes. Peter Conder recalled that Eichstätt turned out extraordinarily good for birds: "John was always the leader and always helpful" he wrote.

The interest in birds and butterflies became so great among the POWs that Buxton posted a weekly report on the notice board in the canteen (Snow, 1990a: 622). These weekly reports are preserved in a notebook entitled *"Natural History Notes. Eichstätt 4 Sep. 1943 to 9 Dec. 1944"*. They contain notes on everything from weather, the arrival of birds, moths, butterflies, and mammals, to star configurations. The reports directed those interested in contributing observations to the appropriate camp specialist: Buxton for birds, Purchon for mammals, as well as others for insects and wild flowers. They also contained miscellaneous notes, such as one notifying readers of the discovery and significance of an *Archaeopteryx lithographica* specimen in a quarry west of the Schloss. The seeds of ambitious but, under the circumstances, impossible, ecological studies appeared as well. One notice announced that notes on birds seen on parole walks would be welcome, as would information on the abundance of voles in various areas: "If possible the number of holes in a square yard should be counted", resulting in Buxton admitting that the naturalists provided a "source of merriment" to some of their fellow prisoners.

Notified of his endeavours, friends and ornithologists back home sent Buxton information on redstarts. Eventually he obtained some scientific journals and bird rings, difficult to get even in England, from the ornithologist Erwin Stresemann in Berlin (Lockley, 1947: 195). Buxton later recalled how the great German ornithologist "gave us all the help he could", writing numerous helpful letters "when to do so risked incurring the dangerous displeasure of the authorities", and putting Buxton in touch with other German ornithologists who could help the camp studies (Buxton, 1950: 144).

In January 1945, while Buxton remained a prisoner, his wife Marjorie sent some of the papers he had managed to write to Bernard Tucker, the editor of *British Birds*. She had already organized the publication of a book of his poems, entitled *Such Liberty,* in 1944. Tucker agreed to publish all three papers, notwithstanding the restrictions on paper supplies. Marjorie also sent a paper to the *Quarterly Journal of Forestry,* whose editor noted in reply that although the journal did not usually publish articles on birds, Buxton's study on redstarts nesting in trees appeared of practical value to foresters.[2] "On the Selection of the Nesting Site by the Common Redstart" duly appeared in the journal in July 1945.

Meanwhile, Buxton's project proved as important to morale in the camp as to his own endurance. Many of his fellow internees, though not enthusiastic bird-watchers, gladly participated in anything to take their minds off their situation and allay that great enemy of the soldier – boredom. Later, some wrote to thank him for the distraction he had provided. One found it very interesting how Buxton later compiled their notes and observations into

readable matter, "providing me with the whole picture which I certainly had not had before".[3] Maurice Waterhouse reminisced in his letter of thanks for reprints: "in reading I found myself constantly back in 'C area' where we wrote, thought, or talked Redstarts, Redstarts, Redstarts".

Buxton reminisced modestly, even cynically, about his critical role in both the ornithology of the prison camps and the observatories: "I suppose I was the leading spirit in the ornithology of prison camps, merely because I contrived to get myself into them before anyone else – I don't know if such a fact is of any interest: it is obviously not a matter of much pride, as it was merely an unhappy accident".[4]

Ornithologists later wrote that, in addition to inspiring a few individuals, the work in the camps influenced British ornithology over the long-term as well, providing "nurseries for many of the next generation of leading ornithologists" (Bourne, 1989: 158). The British bird observatories developed in the 1940s and 1950s became the most enduring legacy of plans made by Buxton and his fellow POWs. A few bird observatories had been in operation in Europe long before the war, established in strategic points along migration routes where birds could be ringed and released in concentrated numbers. The ornithologist Heinrich Gätke had founded the first observatory at Heligoland, and Lockley's Skokholm Bird Observatory and the Midlothian Ornithological Club's observatory on the Isle of May emulated his work prior to World War II. The work at these stations came to a halt with the outbreak of the war, but, as Lockley wrote, "the fortune of war was to make some strange opportunities".[5]

John Buxton and his friends began discussing the future of the observatories while in prison, and upon returning home organized their recovery on Skokholm and the Isle of May, and opened a new one on Fair Isle. Soon after returning home Buxton visited Lockley at Island Farm on Skokholm in the company of two experienced organizers of naturalist groups, Julian Huxley and Max Nicholson, while Waterston arranged visits by ornithologists to Fair Isle to discuss the possibility of a bird observatory there as well. Waterston wrote to Buxton that he looked forward "with keen interest to hearing the outcome of the talk with Huxley, Nicholson, Lockley and yourself on the subject of Bird Observatories".[6] By February 1946, W.B. Alexander, Buxton, Lockley, Waterston, and others had formed the Bird Observatories Sub-Committee of the British Trust for Ornithology. When the task of actually running the observatories soon passed to the West Wales Field Society, the Society hired Buxton as the first warden on Skomer Island, a sub-reserve of Skokholm. Three of his fellow ex-POWs already held similar positions: Peter Conder on Skokholm, John Barrett at nearby Dale Fort, and Frank Elder at a third observatory. Buxton later recalled in a lecture how one of his fellow naturalist-inmates had been amazed that the observatories materialized out of the dreams of idle prisoners ("Fungus, flora and mice: natural history activities", *Wiltshire Herald & Advertiser*, 25 November 1955).

Naturalists credited Buxton's work, and the work he inspired others to do, as leading to two of the main developments in field work, namely, the co-operative study either of a species or of migration by a team of people, and the work of the bird observatories. This work, Buxton later wrote, "has pretty closely followed an article I sent home from prison and which has been organized by a committee – which I initiated – the only one I ever will! – whose first meeting was held in my house!"[7] Although by June 1948 Buxton had written to Waterston that he would have to discontinue his involvement with the bird observatories owing to the pressure of his position as a junior lecturer in English at New College, he pursued the idea of publishing his work on the redstarts.

His ornithological friends encouraged him and he began preparing a book for the 'New Naturalist' series, founded in 1945 to produce popular yet scholarly, well-illustrated works of British natural history. The series would eventually include books by some of the pioneer students in behaviour, including N. Tinbergen and R. Hinde. Buxton obviously felt somewhat uncomfortable submitting his observations to print. James Fisher, the zoologist editor of the series and a good friend, had endless trouble with Buxton's constant pleas that

he was not a scientist. "You have definitely overdone the 'mere naturalist and not a scientist' attitude," Fisher wrote, "Can you please do something mildly about it?"[8] The constraints of having observed from a prisoner-of-war camp created one source of Buxton's doubts. He thought the map of redstart territories made at Laufen too inaccurate since it relied largely on guesswork "owing to barbed wire and all that". And he did not believe the song chart of much value "except as a summary for my own use when writing the book – simply because we were not allowed out in the early hours when song was pretty certainly maximal".[9]

It is important to note that Buxton wrote while ornithological reformers like David Lack were transforming 'scientific ornithology' from museum-based studies to a focus on the living bird in its natural environment. While he agreed on the importance of studying living organisms, Buxton often expressed disapproval of both the methods and the aims of these reformers. In his introduction to *The Redstart*, a meticulous study of the behaviour of four pairs of redstarts during the breeding season, Buxton remarks: "We were not scientists, not trained in school and university to the technicalities of biology, but mere naturalists who delighted in the birds and were content to note down what we saw or heard without any opinion about its significance" (Buxton, 1950: 2). A few pages later he wrote: "If others can interpret my record more skillfully than I, then I shall be glad. Only I beg that they will go to look at the redstarts, till they know (as I know), that however much satisfaction there may be in tying up facts in neat parcels of theory, there is yet more in the mere observation. I have been content to record what we saw of the lives of these redstarts, which I love for their own sake, and not for the sake of adding to men's knowledge. I write as a naturalist and would here claim no other title" (Buxton, 1950: 4).

Although Buxton was less than happy with some of the results of recent trends in ornithology – he opened up his chapter on "Egg-laying and Incubation" with a tongue-in-cheek reference to the arrogance of those who would, in using birds as biological subjects, create a more 'scientific ornithology' – the explicit focus on the living bird rather than specimens united Buxton and the new professional ornithologists. They found in him a wonderful example of the continued role of the amateur in natural history, in the best tradition of Gilbert White. Huxley, Lack, Tinbergen – all these reformers paid homage to those naturalists who observed birds in the field, and drew upon the tradition of Gilbert White to glorify ornithology's new-found return to the living animal. Of course, as much as ornithological reformers wished to devote endless hours to the meticulous study of the living bird, the 18th century parson's world in which this had been possible was difficult to recreate. It is perhaps ironic that it had taken a world war to enforce the leisure required for such a study.

ACKNOWLEDGEMENTS

I am most grateful to David Allen, Keith Benson, Erik Ellis, Paul Farber, Mary Jo Nye, Linda Birch, Naomi Behmer, Caroline Dalton and Trevor Kerry for their help and encouragement.

Notes

1 Letter from Buxton to C. Cox, 12 January [1940?]. C. Cox Correspondence, Box 3, New College Archives, [NCA].
2 Notes on the Common Redstart Eichstätt 1943: 1 April to 27 May, Nests 17, 16, & 19 (Same pair); Notes on the Common Redstart, Eichstätt 1943: 27 May to 30 September, Nests 19 & 22 (Same pair). John Buxton Archives of the Alexander Library, Edward Grey Institute of Field Ornithology, University of Oxford [JBA].
3 Letter from W. E. Hitley to Mrs Buxton, 20 March 1945 [JBA].
4 Letter from Philip ___ (illegible), 24 October 1945 [JBA].
5 Letter to James Fisher, 21 February 1949 [JBA].
6 Lockley, R., "British bird observatories: revival and extension of bird-marking work". Typescript [JBA].

7 Letter from George Waterston, 10 July 1945 [JBA].
8 Letter from Buxton to C. Cox, 16 October 1952 [NCA].
9 Letter from James Fisher, 11 June 1948 [JBA].
10 Letters to James Fisher, 6 September 1948 & 4 October 1948 [JBA].

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BOOK REVIEWS

Mayfly Larvae (Ephemeroptera) of Britain and Ireland: keys and a review of their ecology by **J.M.Elliott** and **U.H.Humpesch.** Pp.152, with 54 figures & 7 colour plates. Environment Agency & Freshwater Biological Association. 2010. £27.00 paperback (plus postage), from: FBA, The Ferry Landing, Far Sawrey, Ambleside, Cumbria LA22 0LP.

The ancestry of this work begins in 1942 with a handbook in the same series by Kimmins which included keys to British mayfly larvae at the generic level. Then came Macan's key to species in 1961, with revisions in 1970 and 1979, and a much updated revision by Elliott, Humpesch and Macan in 1988, following Macan's death in 1985. This latest revision by the first two authors, dedicated to Macan, is in an enlarged format, embraces 51 species – three more than the previous edition – and brings the nomenclature up to date. As well as the excellent drawings of living larvae by Mizarro, a dozen species are illustrated by colour photographs. A 43-page section on the biology of larvae provides a vast amount of updated information for the mayfly enthusiast. GF

Hope for Animals and their World: how endangered species are being rescued from the brink by **Jane Goodall**, **Thane Maynard** and **Gail Hudson**. Pp. 392, with 45 colour & 69 b/w photographs. Icon Books. 2010. £17.99 hardback.

The subject of this book, exemplified in its sub-title, is a fascinating account of the efforts of environmental researchers and conservationists around the world to combat, against all odds, the alarming rates of species extinctions.

Presented as a series of case studies featuring 35 species (15 mammals, 15 birds, two reptiles and one each of beetle, fish and amphibian), this book provides fascinating insights on this sample of conservation projects; more particularly it includes first hand accounts from those who have often risked their lives and welfare for their various wildlife causes, Dame Jane Goodall herself being a prime exemplar.

It is both heartening and heartrending to be made aware of the heroic activities of these highly motivated, selfless, devoted individuals who are trying to salvage a few living gems from the global ecological wreckage, wrought by the rapacious material demands of our society, and the unsustainable lifestyles to which the world's burgeoning human population is encouraged to aspire. This book will make an excellent Christmas present and one that will stand a good chance of being read. CAH

THE NORTHERN BOTTLENOSE WHALE *HYPEROODON AMPULLATUS* (ODONTOCETI: ZIPHIIDAE) IN YORKSHIRE WATERS, WITH NOTES ON ITS MIGRATION, FEEDING ECOLOGY AND THE DISCOVERY OF PHOTOGRAPHS OF THE STRANDING AT SPURN 28 JULY 1930

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INTRODUCTION

North eastern Atlantic status

The northern bottlenose whale *Hyperoodon ampullatus* Foster is only found in the north Atlantic. A cold-temperate to sub-arctic species, moving in summer to polar waters, it feeds principally on squid of the genus *Gonatus* at depths of up to 1450 m, and may even descend deeper than sperm whales (*Physeter macrocephalus*), with dives of 70 min. having been recorded (Bonner 1989, Hooker & Baird 1999). It is most commonly recorded off western Norway and in the Barents Sea.

British status and strandings around the North Sea coasts

The northern bottlenose whale also occurs in small numbers along the continental shelf break west of Ireland, around the Western and Northern Isles of Scotland and as vagrants in the northern North Sea where it is the largest of the beaked whales (*Ziphiidae*) to visit these waters. Relatively few groups enter the North Sea, though strandings are reported from the coasts of Denmark (Kinze *et al.* 1998), the Netherlands (Boschma 1950, Kastelein & Gerritis 1991), Belgium (De Smet 1974) and France (Duguy 1990), however the shallow southern North Sea is unlikely to be part of its normal range. There are also occurrences on the Scottish and English North Sea coastlines (Hooker *et al.* 2008), with the Yorkshire and Humber having a noticeable concentration of stranding records (Spalding 1966, Delany 1985, & this study).

Yorkshire records (Tees to Humber), with clarification of some regularly repeated errors

The discovery of three photographs of a northern bottlenose whale stranded on the Humber shore of Spurn Peninsula instigated this review of occurrences in Yorkshire waters in order to determine whether this represented a hitherto undocumented occurrence or if it provided additional information to that appearing in the literature. The opportunity has been taken to map the known records, to look for patterns in temporal occurrence and size distribution and to discuss reasons for its occurrence.

RESULTS

Although most of the following occurrences are listed in the main reviews of Yorkshire cetacea (Clarke & Roebuck 1881, Grabham 1907, Spalding 1966, Delany 1985, Howes 1996, 2000), by definition these are abbreviated and in certain instances have perpetuated accumulated errors. This study attempts to resolve erroneous reportings and where possible to refer to original and more complete literature sources.

July 1826. A young male specimen was killed in Goole Docks (SE/7423) on the occasion of the first opening of the lock gates. The mounted and cased jaws are in the collections of Goole Museum (Redman 2004).

1837. A female stranded near Hull (TA/02). Its skeleton, measuring17 ft 6 in (4.5m) in length, was displayed in the museum of the Hull Philosophical Society (Thompson 1837, Grey 1866, Clarke & Roebuck 1881, Redman 2004).

[**Pre-1863**. Spalding (1966) erroneously listed a specimen with the unlikely length of 45 ft, stranded on Whitton Middle Sands prior to 1863. This record was reiterated in Delany (1985) and Howes (2000). Not only was the stated length too great for *H. ampullatus*, the original source of this record (Morfitt 1899) showed the figure 45 related not to a length but to an estimation of the number of stranded whales. Further, it is likely that Morfitt's recollection referred to an earlier mass stranding of 42 (not 45) long-finned pilot whales (*Globicephala melaena*) (not northern bottlenose whales *H. ampullatus*) which stranded on Whitton Sands in June 1862, part of a larger group which occurred in the Humber area, some of which also stranded at Cleethorpes (see Limbert 1985)].

Summer of 1863 or 1864. 23 of a school of 25 were hunted and killed in the Ouse at Goole (SE/7423) (Bunker 1882, 1898, Morfitt 1899, Spalding 1966, Howes 1996, 2000). One of these, killed in Goole Docks, measured 15 ft (4.57 m) and weighed 1 ton and 5 cwt (1,270 kg) (Morfitt 1899). Their identity was confirmed as *Hyperoodon ampullatus* after two teeth were identified by C.W. Andrews of the British Museum (Nat. Hist.) (Sheppard 1899, Limbert 1985). Limbert (1985) also noted that these were later erroneously reported as pilot whales *Globicephala melaena* by Bunker (1905) and bottle-nosed dolphin *Delphinus tursio* by Grabham (1907).

September 1867. An adult female and young at the mouth of the Ouse (SE/8623) (Turner 1886, Roebuck 1893). Spalding (1966) mistakenly quotes this record as referring to eight females, an error reiterated in Delany (1985) and Howes (2000).

1877. A 15 ft (4.57 m) specimen stranded in the Trent which was one of 'several' seen in the river between Amcotts (SE/8514) and Keadby (SE/8311). A few days later the remainder of the group had returned downstream and had entered the Ouse (Peacock 1901).

1880. A 28 ft (8.53 m) specimen stranded at the mouth of the River Hull (TA/1028) (Howarth 1880). Though claimed to be a female, its length is at the upper limits for its sex and well within the range for adult males. Curiously, although the reference was cited by Clarke and Roebuck (1881), they omitted the record.

1880. One stranded at Patrington Haven (TA/3318) was skeletonised on site, brought to Hull and articulated by a Dr Foster (of Hull) before being sold to an unnamed private collector (Howarth 1880, Clarke & Roebuck 1881).

Pre-1886. The skull of a specimen which stranded at Whitby 'many years ago' is in Whitby Museum (Stephenson 1886).

13 March 1888. After prolonged violent gales and rough seas a 16 ft (4.8 m) specimen stranded at Danes Dyke (TA/2169) (Bailey 1888).

9 July 1890. A 20 ft (6.1 m) specimen was caught in salmon nets and badly injured by fishermen before being released into the Tees estuary at South Gare, Teesmouth (NZ/5427) (Nelson 1890).

13 December 1910. A 25 ft (7.6 m) specimen stranded at 'The Station' (presumably the coastguard station) Spurn (TA/4011) was cut up and buried by the coastguards (Grabham 1911).

28 July 1930. A specimen about 22 ft (6.7 m) in length, was stranded alive at 9.30 am on the western side of Spurn Peninsula. An attempt to get it into deeper water on the next tide failed owing to its weight (Bramley 1931). Figures 1, 2 and 3 show the whale beached on the Humber foreshore of Spurn Peninsula almost certainly refer to the individual recorded in the literature, Figure 1 showing the precise stranding site to be Chalk Bank (TA/4112). The images are from a collection of family photographs owned by the Hildred family who were then resident in Grimsby and who were, about that time, enjoying a fortnight's summer holiday at Spurn in a wooden bungalow close to the Spurn lighthouse. Trevlynn Hildred, who supplied the photographs, was eight years old at the time and understandably has only a few hazy memories of the holiday, which she dates to **1930 or 1931.** She remembers little of the actual stranding other than to recall that "great efforts were made to refloat the whale" while it was still alive. The photographs were taken by her father, Frederick Hildred.

16 August 1938. A 21 ft 1½ in (6.4 m) specimen stranded in the Trent at Keadby (SE/8311) (Gallwey 1939). Its skull (no.SW.1938.25), recorded under the provenance of Gunness, where it was brought ashore, is in the collections of the Natural History Museum, London (Redman 2004).

12 December 1942. A 26 ft (7.9 m) specimen stranded in Robin Hood's Bay (NZ/9504) (Spalding 1966, Delany 1985).

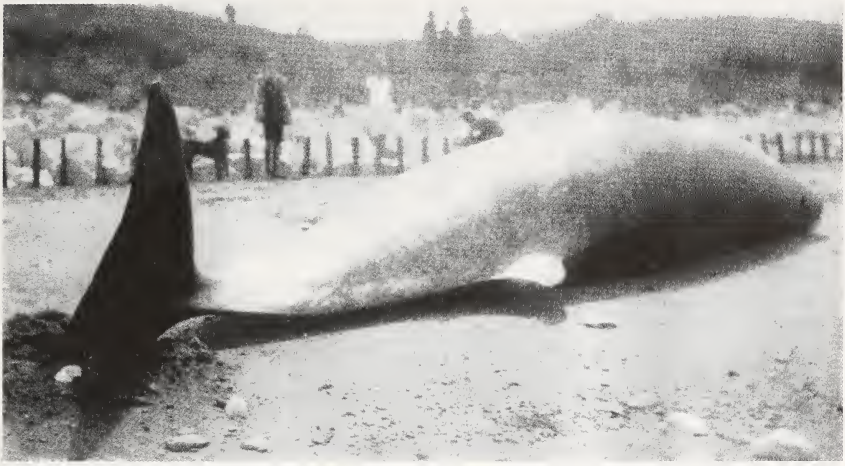

FIGURE 1. Bottlenose Whale. Dorsal view showing the tail, characteristically without a central notch and the sickle-shaped dorsal fin, with Spurn's Chalk Bank in the background.

FIGURE 2. Anterio-ventral view: showing the pronounced bulbous forehead with small colony of barnacles, *Balanus* sp., the 'beak' and the characteristic diverging longitudinal throat grooves.

FIGURE 3. Ventral view: showing the 'beak', throat grooves, the thoracic area and abdominal region with the urino-genital and anal openings.

13 July 1943. A 20 ft 6 in (6.2 m) specimen stranded at Marske (NZ/6523) (Spalding 1966, Delany 1985).
13 July 1943. A 20 ft 6 in (6.2 m) specimen stranded at Marske (NZ/6523) (Spalding 1966, Delany 1985).
14 August 1958. One was killed when struck by a ship in the Tees estuary (NZ/5220) (Coffey 1977).
July & August 2004. One washed up several times over a 3-day period in the Ouse between Saltmarshe (SE/7823) and Goole (SE/7523). On 2 August it finally stranded on the sandbank beneath the M62 Ouse Bridge near Howden (SE/7426) (*Goole Times* 5 & 13 Aug. 2004, illus.).

DISCUSSION AND CONCLUSIONS

Geographical distribution

Figure 4 summarises the stranding sites, indicating an orientation to estuaries (Tees & Humber) and tidal river systems (Hull, Ouse & Trent). Whether this can be explained by whales pursuing inward migrations of anadromous fish or by futile attempts to travel west to correct their migratory disorientation, awaits further research.

Temporal distribution

Figure 5 shows the temporal distribution over 19 decades from 1820 to 2009, indicating that vagrant occurrences are extremely scarce, averaging at c. 8 events and 22 individuals per century.

Population composition

According to length categories for adult females (7.0-8.5 m) and for adult males (8.0-9.5 m) (Hooker *et al.* 2008), of the 11 recorded length measurements (see Fig. 6), eight were juveniles and three were adults, of which one at least was a female and one was possibly a male.

Migration patterns and the seasonality of strandings

Dated occurrences in Yorkshire waters are from the following months (number of specimens in parenthesis): December (2), March (1), July (4), August (3) and September (2) with the mass stranding of 1863 or 1864 taking place during summer. This shows that although

vagrants can occur during any season, there is a discernable summer (July to September) concentration. Through the examination of historical strandings data from the United Kingdom and the Republic of Ireland, and of whaling records from the Faroes, Iceland and the Norwegian Sea, MacLeod and Reid (2003) have provided strong evidence that *H. ampullatus* undertakes regular migrations, moving north-east in late winter and spring and south-west in late summer and autumn. Reyes (1991) shows that in the eastern North

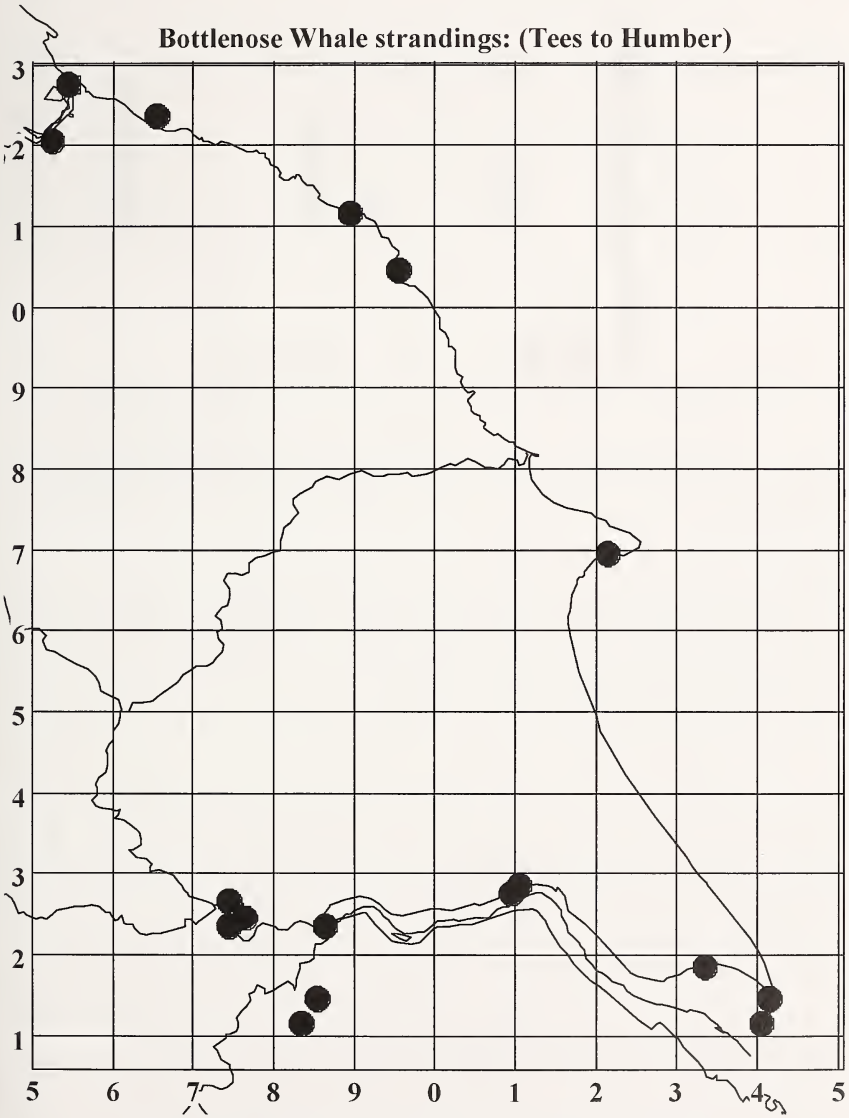

FIGURE 4. Stranding sites in Yorkshire waters (Tees to Humber).

Atlantic a southward migration from the Norwegian Sea begins in July and continues to September. Although *H. ampullatus* occur all year round in the Faroes, Bloch *et al.* (1996) observed a distinct peak of occurrence a fortnight around 1 September demonstrating a highly synchronized southerly migration movement. The seasonal pattern of strandings on the British and North Sea coasts probably reflects part of this late summer migration.

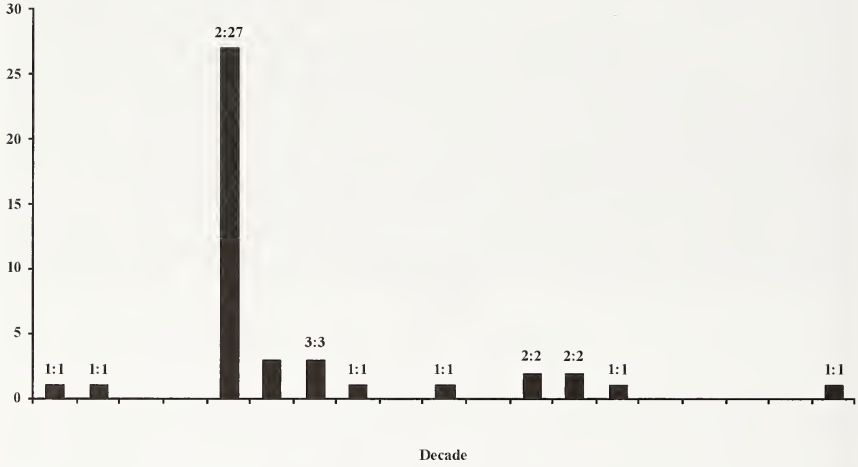

FIGURE 5. Northern Bottlenose Whale records per decade in Yorkshire waters (Tees to Humber). Values refer to a) number of stranding/sighting events and b) estimated number of specimens.

Diets

Traditionally frequented feeding areas in the eastern North Atlantic are the Shetland-Faroes Channel and an area to the south-west of the Faroes including the northern end of the Rockall Trough (MacLeod & Reid 2003). Stomach content analysis by Clarke and Kristensen (1980) on a specimen stranded on the Faroe Islands showed that while the cephalopods found included six cold water species which were probably taken in deep water within the vicinity of the Faroes, they also included one species, *Vampyroteuthis infernalis*, which is a warmer water species and probably ranges little further north than 40°N. The stomach contents of the Faroese specimen also showed more diversity, with 13 species eaten, than those from a whale stranded in Denmark (Clarke & Kristensen 1980). From within the North Sea basin, Santos Vázquez *et al.* (2001) examined the stomach contents of a juvenile male northern bottlenose whale stranded in November 1885 at Dunbar (Scotland), a male stranded in February 1997 on the island of Tåsinge (Denmark) and two females stranded on the Dutch coast, one in August 1956 on the island of Texel and one in August 1993 at Hargen. Food remains from the four samples consisted almost entirely of cephalopod beaks, the species range consisting mainly of oceanic taxa. These were *Gonatus* sp. (probably *G. fabricii*), *Taonius pavo* and *Histioteuthis* sp. for the Dunbar whale; *Gonatus* sp. and *Teuthowenia megalops* for the Texel whale; *Gonatus* sp. for the Hargen whale and *Gonatus* sp., *T. megalops* and *Taonius pavo* for the Tåsinge whale. Other prey species found in the Tåsinge specimen included the squid *Histioteuthis reversa*, *H. arcturi*, and the octopods *Vampiroteuthis infernalis* and *Vitreledonella richardi*. Based on the size of the lower beaks, the squid eaten included juvenile and mature individuals of the most important taxa (*Gonatus* sp. and *Teuthowenia megalops*). Occasional fish remains consisted of vertebrae of Gadidae (cod family) and fish eye lenses (from the Hargen whale)

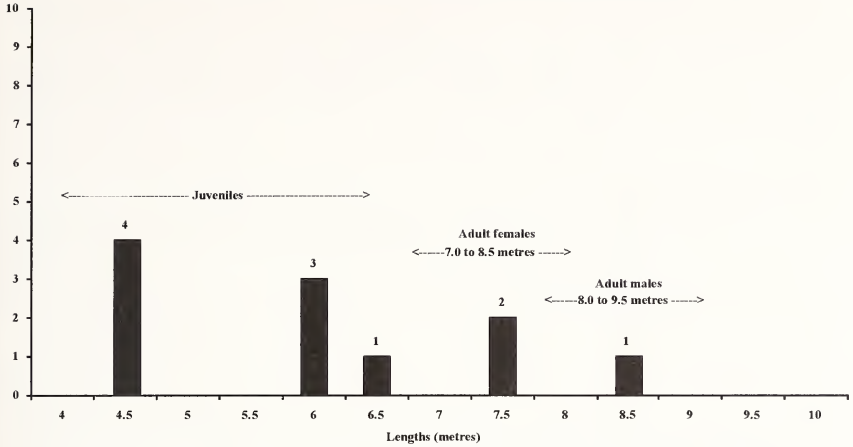

FIGURE 6. Length ranges of Northern Bottlenose Whales stranded in Yorkshire.

and two *Trisopterus* sp. (Pouting) otoliths (from the Tåsinge whale). The results from this study suggest that cephalopods in general, and *G. fabricii* in particular, are the main prey of the northern bottlenose whale in northern latitudes and that little or no feeding takes place within the southern North Sea.

In that occurrences of toothed whales (Odontoceti) in the Humber/Ouse/Trent system have historically been attributed to their pursuit and consumption of inward migrations of salmon (*Salmo salar*), this has led to salmon fishing interests understandably but erroneously offering bounties to encourage their slaughter (Howes 2008). It is likely from the diet analyses of Clarke and Kristensen (1980) and particularly Santos Vázquez *et al.* (2001) that salmon would probably not have been the quarry of northern bottlenose whales. Further, considering the residual, possibly functionless, dentition of northern bottlenose whales, which consists of a pair of stubby teeth in the lower jaw, which in females do not even erupt (Bonner 1989), and with Thompson (1838) making the point that in the Hull 1837 specimen, the pair of teeth were 'entirely concealed by the gums' and therefore had not erupted, it is unlikely the whales would have been able to effectively catch and hold salmon.

Acknowledgements

Our thanks are due to Trevlynn Hildred for the photographs which instigated this study, Angela Gowland (Hull Naturalists' Society) for the press cuttings of the 2004 stranding, Joanne Chilman (Hull History Centre) for the 1899 William Morfitt reference, Martin Limbert (Doncaster Museum and Art Gallery) for access to Doncaster Museum's runs of *The Naturalist* and Dr Graham J. Pierce (School of Biological Sciences, University of Aberdeen), for his generous advice on distribution and feeding ecology which led to significant revisions to this study.

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SPERM WHALE *PHYSETER MACROCEPHALUS* STRANDINGS ON THE CLEVELAND, NORTH YORKSHIRE AND HUMBER COASTLINES

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Sperm whales (*Physeter macrocephalus*) in the Northern Hemisphere exhibit a high degree of geographical segregation between sexes. Pods of females with calves stay on or near the breeding grounds throughout the year, roughly between 40-45°N and 40-45°S (Rice 1989, Whitehead 2003, Pierce *et al.* 2007). During the summer months, male sperm whales undertake long migrations between low-latitude breeding areas and high-latitude feeding grounds, feeding in mid-ocean over submarine canyons or at the edges of the continental shelf. "Bachelor" groups comprising young and adult male sperm whales, as well as old bulls not taking part in reproduction, usually leave warm waters at the beginning of summer and migrate to feeding grounds that may extend northwards as far as the edge of Arctic waters. In autumn and winter, they generally return southwards, although some may remain in colder waters during the greater part of the year (Pierce *et al.* 2007). During the summer months, some of these male sperm whales appear off the west coast of Ireland and Scotland. Occasionally, but with increasing regularity, the groups round the north coast of Scotland and effectively become 'trapped' in the shallow waters of the North Sea.

Sperm whale strandings are distributed around the North Sea coasts, especially on the shallower coastlines of Denmark (*19 stranding sites), Germany (13), Holland (17),

Belgium (10) and France, south to the Straits of Dover, (2). The 38 stranding sites on the British east coast (15 Scottish & 23 English sites) become more concentrated south of latitude 53°N from Holderness, the Lincolnshire and East Anglian coastlines. [*Figures in parenthesis represent approximate numbers of stranding sites illustrated in Pierce *et al.* 2007.]

North Sea strandings have been recorded since the mid-16th century, and tend to be clustered chronologically. The most notable peaks, both in terms of the number of years in which strandings occurred and in the total number of whales stranded, were in the second half of the 18th century and at the end of the 20th century (Smeenk 1997, 1999), the latter cohort leading to much speculation about causes. In the 20th century, all the recorded sperm whale strandings in the North Sea are known to have been males ranging in age from 12 to 57 years, the majority being 20-36 years, some stranding in groups of up to 16 animals.

To date, only nine fatal strandings in Cleveland, North Yorkshire and Humber waters (from the Tees to the Humber) are known (Fig. 1). Interestingly, the first documented British record was of a single whale that entered the Humber in 1563, finally stranding at Grimsby (Roebuck & Clarke 1884/5, Smith 1905, Anon. 1910, Blathwayt 1912, Spalding 1966, Howes 1996, 2000).

1795 Redcar (NZ/62) One stranded at Redcar in July 1795 "... a spermaceti whale was driven ashore ... it measured fifty feet, and was claimed by Lord Dundas" (*Doncaster Journal & Yorkshire Advertiser* 25 July 1795).
1825 Tunstall (TA/3132) A specimen stranded on 28 May 1825. Through the title of Lord Paramount of the Seigniory of Holderness, the Chichester-Constable family of Burton Constable Hall held the right to any creature which beached between Flamborough Head and Spurn. The specimen was therefore taken to the Hall where its skeleton still survives (Anon. 1910, Spalding 1966, Delany 1985, Howes 1996, 2000).
1937 Bridlington (TA/16) The skeleton of one which stranded on 25 Jan. 1937 was removed to the Natural History Museum (Clarke 1937, Fraser 1946, Spalding 1966, Delany 1985, Howes 1996, 2000).
1993 Atwick (TA/1951) A 50ft male with an estimated weight of 15 tonnes was stranded on 15 Dec. 1993. Teeth removed for sectioning determined the animal's age to be 35 years (Howes 1996, 1997, 2000, *Hull Daily Mail* 16 & 17 Dec. 1993, *Yorkshire Post* 17 Dec. 1993 illus.).
1994 Hawsker Bottoms (NZ/9307) A 30 ft male was stranded on 13 Nov. 1994 (*Yorkshire Post* 6 Nov. 1994). Possibly related to this incident was the fatal stranding of a 52 ft male in the Wash near Gibraltar Point, Lincolnshire on 15 Nov. 1994 and 11 in the Orkney Isles during the 1st week of December 1994 (Natural History Museum Cetacean Stranding Website).
1997 Humber mud inside Spurn (TA/41) Two large dead specimens were stranded on 3 Dec. 1997 (*Hull Daily Mail* 4 Dec. 1997, *Yorkshire Post* 4 Dec. 1997 illus., 6 Dec. 1997 illus.). These were evidently from a much larger group, 20 of which were stranded at various points around the North Sea basin during the first week of December (13 on the Danish island of Rømø, 2 on the north German coast, 5 along the Dutch coast) (Smeenk 1999).
2003 Sperm whales would have passed through Yorkshire waters in 2002-2003, with one stranding at the mouth of the Great Ouse in Norfolk on 26 Jan. 2003 (Natural History Museum Cetacean Stranding Website).
2006 Kilnsea mud (TA/41) A 30 ft specimen was stranded alive on the Humber mud 1 mile west of Kilnsea at c. 10.00 am on 4 Feb. 2006. It was 'blowing' in shallow water at that time, but was stranded and embedded in the mud as the tide fell by 3.00 pm. (*Yorkshire Post* 6 Feb. 2006). This was part of a larger group that entered the North Sea. Three more were fatally stranded on the Lincolnshire coast (2 at Gat Sands on 6 February and 1 at Skegness on 15 February).

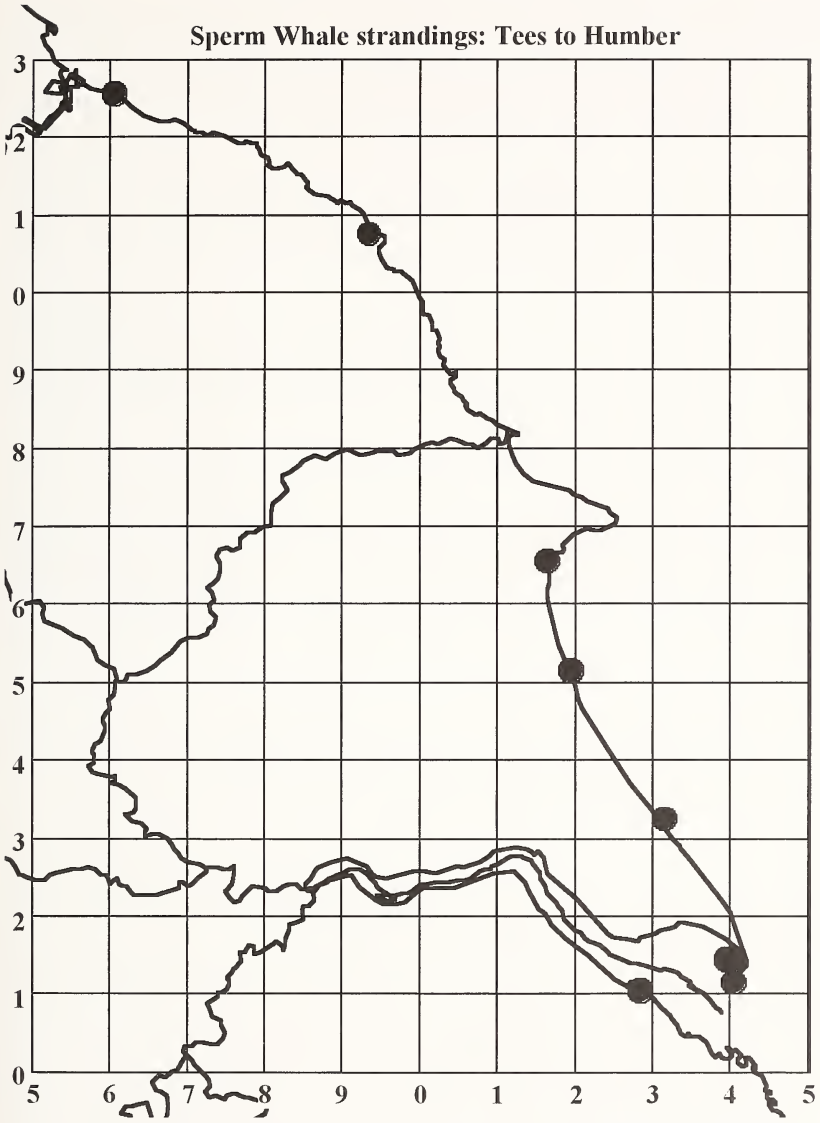

FIGURE 1. Locations of Sperm Whale strandings in the Yorkshire and Humber region.

Discussion

Diet studies have shown that whilst in deep sub-arctic and arctic waters of the North Atlantic, a major food source for many top predators, including sperm whales, is the Arctic squid *Gonatus fabricii* (Bjørke 2001, Pierce *et al.* 2007). Although Sperm whales stranded

in the North Sea during the 1990s had previously been feeding largely on *G. fabricii* (Santos Vázquez *et al.* 1999, 2002, Simon *et al.*, 2003), the species itself does not occur in the North Sea. Santos Vázquez *et al.* (1999) found that the stomachs of sperm whales stranded in the North Sea were full of *Gonatus* beaks, providing evidence of feeding in the Arctic and sub-Arctic; however, there were few remains of coastal cephalopods or fish, with only single beaks of the squid *Loligo forbesi* and the octopus *Eledone cirrhosa* and a bone from a gadid fish, and probably a saithe *Pollachius virens,* which showed little evidence of feeding in the North Sea. In stomach samples from two sperm whales collected in the Netherlands in 1997, Santos Vázquez *et al.* (2002) found remains of saithe and monkfish *Lophius piscatorius*. These species represented a very small fraction of the stomach contents, which otherwise contained remains of *Gonatus* and other northern species presumably consumed prior to entering the North Sea.

Although sperm whales are important predators in deep oceanic waters, they are poorly equipped for foraging and navigating in shallow waters, their echo-location being poor at detecting gently sloping sandy shores (G.J. Pierce *pers. comm.*). This is consistent with Smeenk's (1997) observation that most multiple strandings occur in the southern part of the North Sea in places characterised by mud flats and estuaries, and that the North Sea effectively functions as a sperm whale trap.

Informal discussions instigated by the author's poster display at the Yorkshire Naturalists' Union Conference on the Yorkshire Coast (March 2004) speculated that sperm whales may feed preferentially on 'giant squid' (*Architeuthis* sp.) and that their occasional presence in the North Sea could be in pursuit of vagrant *Architeuthis clerckei* (Robs.), the type specimen of which was stranded at Scarborough in January 1933 (Clarke 1933). This is not supported by evidence from stomach contents. Dr M. Begoña Santos Vázquez and

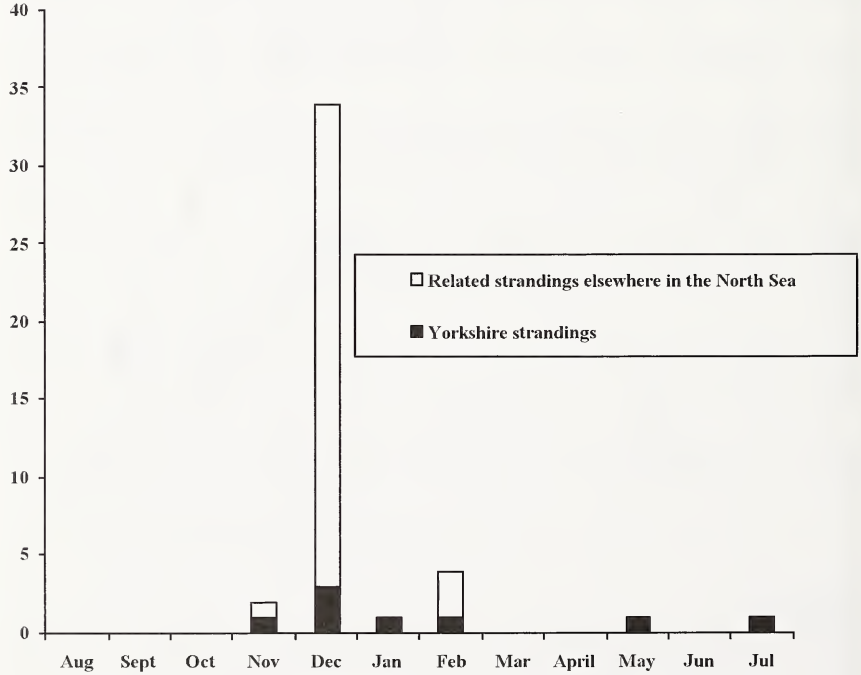

FIGURE 2. Seasonality of Sperm Whale strandings on the Yorkshire coast.

Dr Graham J. Pierce (*pers. comm.*) point out that only two *Architeuthis* beaks have been recovered from sperm whale stomach contents studied around the British Isles and these were from a single sperm whale stranded on the Irish coast.

Most North Sea strandings have occurred in the period November to March (e.g. 69 of 74 animals in 1990-1999) apparently during or some time after the southward migration (Smeenk 1997, 1999). Figure 2 shows that Yorkshire strandings accord with this pattern.

Acknowledgements

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ROBERT FRANCIS DICKENS
1918 – 2010

Bob Dickens was born at Stewkley in Buckinghamshire on 30 March 1918. The son of a farm worker and sometime butcher, he developed an interest in nature at an early age. From the village school he went on to the local grammar school where he played rugby union as a full back, an activity seemingly at variance with the quiet, unassuming man we in Yorkshire came to know. He attended Goldsmiths College in London before starting his teaching career in Guildford, Surrey.

At the outbreak of World War II, he registered as a conscientious objector and, alongside his teaching role, joined the ambulance service. At the end of the war, he moved north to join the staff of the Brontë High School in Leeds, before moving to Crewe Road Secondary Modern School (now Airedale High) in Castleford. Initially he taught mathematics and rural studies, but later concentrated on the latter, introducing his pupils to many aspects of the natural world, something which, but for his enthusiasm, they might otherwise never have experienced in this industrial region. He maintained a school greenhouse where exotic plants were grown and also, with the headmaster's permission, built an enclosure in which were kept chickens and wayward Canada Geese.

Bob Dickens with juvenile Great Black-backed Gull, Iceland, 1959.

His interest in birds led him to spend much of his leisure time at Spurn and at Fairburn Ings, then an expanding area of mining subsidence flashes with which his name would eventually become synonymous. In 1957, together with his friend Dr J.D. Pickup, he persuaded the West Riding County Council and the National Coal Board to designate the area as a Local Nature Reserve, which was then monitored by a group of voluntary wardens under his chairmanship. In 1973, he and Pickup wrote *Fairburn and its Nature Reserve* (Dalesman Publishing). During the late 1960s and early 1970s, he was the area representative for the Royal Society for the

Protection of Birds; through his unstinting efforts, the importance of Fairburn, particularly for breeding and migrating birds, was recognized and the RSPB took over its management in 1976. In the Reserve's Annual Report for 1978 he wrote of 'The first 21 years', which gives a most detailed account of the inception and development of this nationally important reserve. His contribution to Fairburn Ings cannot be overstated and the award of the RSPB's Silver Medal for Nature Conservation was a very well deserved honour for this dedicated man.

His name first appeared as a contributor to the Ornithological Report of the Yorkshire Naturalists' Union in 1947 when he was credited with seeing 11 Little Stints at Spurn on 24 May; many other contributions to the Bird Report followed. In 1954, he became Secretary of the Union's Ornithological Section, a post he held until 1971, becoming Chairman in 1972. He also served for many years on the Protection of Birds Committee. He was a regular contributor to *The Naturalist*, submitting many short papers and field notes on a wide diversity of subjects. Elected to the Presidency of the YNU in 1964, his Presidential address on 'Some aspects of bird protection in Yorkshire' was delivered at the AGM on 5 December 1964 in Halifax.

Alongside his involvement at Fairburn Ings from the late 1940s, he became a regular visitor to the newly established Spurn Bird Observatory where we first met and subsequently became good friends. I vividly recall the early morning of 19 October 1957 when he and I, together with Barry Potter and the late John Weston, were squashed into a small car whilst driving to the Crown and Anchor Inn at Kilnsea for breakfast when I noticed a dead bird lying at the side of the road. The car screeched to a halt and we all exploded therefrom to find what was immediately recognized as a Bonaparte's (now White-rumped) Sandpiper which had presumably hit the overhead wires. Breakfast was postponed whilst we returned to the Observatory to photograph, measure and take detailed plumage notes of the specimen. This Nearctic wader was an addition to the Yorkshire list of birds (*The Naturalist* 1958: 81).

He became a bird ringer, an activity which was first pursued at Spurn Bird Observatory in its early days under the watchful eye of Ralph Chislett. When I first created Knaresborough Ringing Station in the 1950s, Bob visited the area at my request to discuss the siting of the first Heligoland trap, whereafter he took an ongoing interest in the work of the Station. On a visit to Knaresborough in 1963 he photographed a Little Ringed Plover on its nest at nearby Farnham Gravel Pit, the first recorded instance of breeding by this species in the district.

Although not one for globe-trotting, he visited Sweden in the 1950s with his friends Henry Bunce and John Cudworth, and, in association with the Brathay Exploration Group at Ambleside, led expeditions to Foula and Iceland, the latter to study breeding Pink-footed Geese at Thjorsaver, the groups' experiences being detailed in an illustrated lecture to the Ornithological Section of the YNU. On one occasion, whilst returning on a ferry from a visit to the Shetland Isles, he was astute enough to notice that a fellow traveller had birds eggs in his rucksack and so alerted the police who confiscated the hoard which Bob helped to identify.

In the early 1980s, a need to return to Stewkley in order to look after his mother led to his retirement. Once settled, he took an active part in village life, becoming a Parish Councillor and a school governor, and was instrumental in establishing a local conservation area. He was inevitably involved with the local bird club and also the Beds., Bucks. and Oxon. Wildlife Trust, as well as founding the Stewkley Rights of Way Association.

With his return to his place of birth, Yorkshire lost one of its most active and likeable naturalists and was thus deprived of many more years of his dedicated and inspirational involvement in the county's wildlife. For those of us who had known him well and enjoyed the pleasure of his jolly companionship, notably in the early days at Spurn and during his long association with Fairburn Ings, he will be fondly remembered.

John R. Mather

BOOK REVIEWS

Atlas of Rare Birds by **Dominic Couzens**. Pp. 240. incl. many colour photographs & detailed maps. New Holland Publishing, London. 2010. £24.99 hardback.

This large format book details the background and current situation for 50 species of birds throughout the world which are considered to be endangered or under threat of possible extinction. The ten main sections each examine five species under various headings; 'Back from the brink – starting again with just a few survivors', 'The perils of island living', 'Threats in many disguises', 'Migrants in danger – the difficulties of protecting birds on the move', 'Unexpected calamities – once common birds in sudden danger', 'Lost causes – optimism fades', 'Controversies', 'Discoveries', 'Re-discoveries' and 'The pending tray'.

The author examines the plight of each of the 50 species and pontificates on the likely outcomes. There are a few surprises; the Lesser Flamingo, for instance, would seem to be so numerous in its African Rift Valley range that it could be in no danger but there is always a risk in specialization and there is no more specialized bird than the flamingo. Ever increasing human pressures and threats from commercial soda extraction from the main breeding and feeding lakes must surely have a dramatic effect on this enigmatic bird. The author considers the likely consequences for this and all the other threatened species, which makes fascinating, but often disturbing, reading.

Each section begins with a very clear world map showing the location of each of the five species discussed therein and each species in turn has a large scale map of its exact range and an average of four pages of text including some excellent photographs. In an otherwise well written and nicely presented book, it is somewhat irritating to come across a small number of grammatical and etymological errors, and on page 218 we read '...hosts a number of mysterious animals and birds' – surely birds are animals! That said, the book is certainly worth adding to one's library, via the coffee table, offering as it does, a most fascinating and thought provoking read.

JRM

Whitebeams, Rowans and Service Trees of Britain and Ireland. A monograph of British and Irish *Sorbus* L. by **T.C.Rich, L.Houston, A.Robertson and M.C.F.Proctor**. Pp. vi + 223, with 476 colour plates, line drawings, maps & tables. Botanical Society of the British Isles in association with National Museum Wales. 2010. £30.00.

This book is number 14 in the BSBI Handbook Series and deals exhaustively with the very difficult group of apomictic and sexual taxa in the genus *Sorbus*. (Traditionalists will be relieved that the splitting of the genus into five new genera as required by molecular studies is not adopted.) Over the years, the series has changed markedly in character from the original pocket books, with the volumes becoming larger and thicker and more comprehensive; this edition marks a further break by adopting the A4 size seen in recent county floras. The use of colour, essential in the previous volume on fumitories, is here employed to good use for fruit character and for maps and photographs. The illustrations on the whole are of good quality and the inclusion of relevant botanists in some of the photographs is welcome.

The site guide is particularly useful for anyone wanting to travel to see the rarer species, although some would dispute that Humphrey Head is "one of the most wonderful botanical sites in the world". Because of the very limited geographical ranges of some species, those field botanists who confine themselves to Yorkshire could be forgiven for thinking that such a resource as this would be unnecessary, but there is valuable help for identifying the widely introduced and often naturalised species, such as *S. croceocarpa, S. latifolia, S.* x *thuringiaca* and of course the now ubiquitous *S. intermedia*. For the plant "twitcher" who has walked the glens of Arran, or the Wye Valley and the Cheddar and Avon Gorges trying to key out plants using Stace or Clapham *et al.*, this is most certainly

the book they have been waiting for and indeed should be on every serious botanist's bookshelf.

GLDC

CONTRIBUTORS

Abbott, P.P. 20-24, 87-88
Archer, M.E. 84, 92, 93-100, 116, 130-131

Blackburn, J.M. 101, 103, 105, 106
Blockeel, T.L. 109, 114-115
Bowers, J. 129-130

Carr, G. 35-42
Coles, G.L.D. 210-211
Crawford, T. 101, 104
Crompton, H. 100
Crompton, V. 187-188
Crompton, Z. 187-188
Crossley, R. 118
Crowther, P. 195-203
Curtis, B. 85-86

Fletcher, C. 107-108, 111
Fryer, G. 25-34, 92, 135-172, 194

Godfrey, A. 25-34
Goulder, R. 63-73
Grant, D.R. 103, 105, 108, 112, 117
Grayson, A. 101-102, 104-105, 111-112, 116, 127-128

Hemingway, D.G. 134
Henderson, A. 101-117
Higginbottom, T. 102-103, 105-106
Horne, D.J. 25-34
Howes, C.A. 51-62, 74, 83-84, 91-92, 128-129, 131-132, 194, 195-203, 203-208

Johnson, K. 189-194

Lambert, J. 104
Legg, A.W. 103-104
Limbert, M. 131-132
Lindley, D. 107

Malumphy, C. 3-13
Marsh, R. 104, 105, 119-127
Mather, J.R. 134, 208-209, 210
Middleton, P. 35-42
Middleton, R. 15-20

Newbould, J. 106-107, 108-109, 110, 112-114
Norris, A. 89-91, 101-117

Priest, S. 115

Richardson, D.H.S. 43-44

Seaward, M.R.D. 13, 34, 44, 45-50, 133, 173-187, 188
Shields, C.G. 110

Whitaker, T.M. 107, 109, 111
Wilmore, G.T.D. 14, 42-43

INDEX

Arachnology
The hot-house spider *Achaearanea tepidariorum* underground at Brodsworth Colliery, 131-132

Book Reviews
13-14, 34, 42-44, 50, 74, 83-84, 91-92, 100, 128-130, 134, 187-188, 194, 210-211

Botany
Botanical report for 2009, 20-24; Additions to the flora of mid-west Yorkshire, 87-88

Cetacea
The Northern Bottlenose Whale in Yorkshire waters, 195-203; Sperm Whale strandings on the Cleveland, North Yorkshire and Humber coastlines, 203-208

Coleoptera
Coleoptera report for 2002-2009, 119-127

Crustacea
The ostracod *Scottia pseudobrowniana*, an addition to the freshwater fauna of Yorkshire, 25-34

Entomology
A plausible identity for the 'Hinckelhaugh Insect' of John Ray's *Historia Insectorum*, 127-128; George Taylor Porritt's observations on industrial melanism in moths in south west Yorkshire, 135-172

Freshwater Ecology
Aquatic plants in principal drains of the intensively-arable River Hull Valley, 63-73

Hemiptera
Whiteflies (Hemiptera: Aleyrodidae) of Watsonian Yorkshire, 3-13

History
The amazing Mr Sheppard, 45-50; Peter Skidmore (1936-2009): a memorial tribute, 75-83; A naturalist in wartime: John Buxton's pioneering study of the Redstart, 189-194; George Taylor Porritt's observations on industrial melanism in moths in south west Yorkshire, 135-172

Hymenoptera
The wasps and bees of Blaxton Common-2, 93-100; Recorder's tenth report of the aculeate Hymenoptera in Watsonian Yorkshire, 130-131

Lepidoptera
George Taylor Porritt's observations on industrial melanism in moths in south west Yorkshire, 135-172

Lichenology
Lichen flora of the West Yorkshire conurbation: a conspectus, 173-187

Mammals
The Northern Bottlenose Whale in Yorkshire waters, 195-203; Sperm Whale strandings on the Cleveland, North Yorkshire and Humber coastlines, 203-208

Mollusca
Vertigo genesii recorded at Malham, 89-91

Obituaries
Peter Skidmore (1936-2009): a memorial tribute, 75-83; Henry Owen Bunce (1913-2009), 85-86; Kenneth Geoffrey Payne (1917-2010), 118; Robert Francis Dickens (1918-2010), 208-209

Ornithology
The status of moorland breeding birds in the Peak District National Park 2004, 35-42; The Corncrake in southern Yorkshire, 51-62; A naturalist in wartime: John Buxton's pioneering study of the Redstart, 189-194

Pteridophyta
Wall ferns of east Hull, 2004-2008, 15-20

Yorkshire Naturalists' Union
YNU Excursions in 2009, 101-117; Editorial (M.R.D.Seaward), 133

IRISH NATURALISTS' JOURNAL

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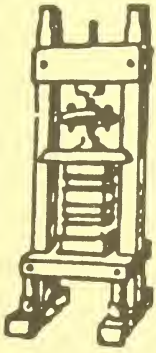

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